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CONTENTS

PAGE

No. 1.—The Size of Parietal Foramen and Organ in Reptiles. A Rectification. By Tilly Edinger. October, 1955 1

No. 2.—A Classification of Therapsid Reptiles. By D. M. S. Watson and A. S. Romer. February, 1956 . 35

No. 3.—The Placenta of the Wolverine (*Gulo Gulo Luscus* (Linnaeus)). By George B. Wislocki and Emmanuel C. Amoroso. (8 plates.) February, 1956 89

No. 4.—The Functional Anatomy of the Delphinid Nose. By Barbara Lawrence and William E. Schevill. (30 figures.) February, 1956 101

No. 5.—Silicified Middle Ordovician Trilobites: The Odontopleuridae. By H. B. Whittington. (24 plates.) May, 1956 153

No. 6.—A Cat Skeleton with an Anomalous Third Hind Leg and Abnormal Vertebrae. By Thomas S. Parsons and John M. Stein. (4 plates.) May, 1956 291

No. 7.—Post-Triassic Nautiloid Genera. By Bernhard Kummel. (28 plates.) July, 1956 319

Bulletin of the Museum of Comparative Zoology

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Vol. 114, No. 1

THE SIZE OF PARIETAL FORAMEN AND ORGAN IN REPTILES. A RECTIFICATION

By Tilly Edinger

CAMBRIDGE, MASS., U.S.A.

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No. 1—*The Size of Parietal Foramen and Organ in Reptiles. A Rectification.*

By Tilly Edinger[1]

CONTENTS

	Page
Introduction	3
Opinions	6
Foramen-eye relations in lizards	11
Literary data	11
Figured data	16
Foramen and skull	19
The size question	19
An answer	20
Application to fossils	24
Summary	29
Literature cited	30

INTRODUCTION

The pineal apparatus consists of one or two organs evaginated from the roof of the diencephalon and their nerve fiber connections with and inside the brain (Fig. 1). Study of such an organ complex would seem a subject altogether inaccessible to students of extinct vertebrates, of which only the hard parts are preserved. This is in great part true of the pineal organ proper (glandula pinealis, epiphysis cerebri), the pineal body which develops in almost all vertebrates. In the extant forms, at least, the epiphysis has no relation to osseous elements of the head, and it is only in some very ancient fishes that the skull bones clearly indicate the presence, above the brain, of two organs in the pineal complex (Edinger, in press). The parapineal organ fails to develop in the vast majority of living vertebrates. In most Lacertilia, however, it is a stalked, dorsomedian, photoreceptive sense organ whose presence is reflected in the structure of the skull roof. Whenever, in a lizard, this parietal organ is well developed as a

[1] This study is one of a series aided by a grant from the Penrose Fund of the American Philosophical Society.

parietal eye, its influence causes and maintains an opening in the bony shield over the brain. This opening is the parietal foramen —always median but variable in position even within species (El-Toubi, 1945, p. 5), lying either between the two parietal bones, between the two frontal bones, or in the fronto-parietal suture (Fig. 4). A corresponding foramen is of frequent occurrence in Paleozoic Agnatha and fishes, and in Paleozoic and Mesozoic amphibians and reptiles.

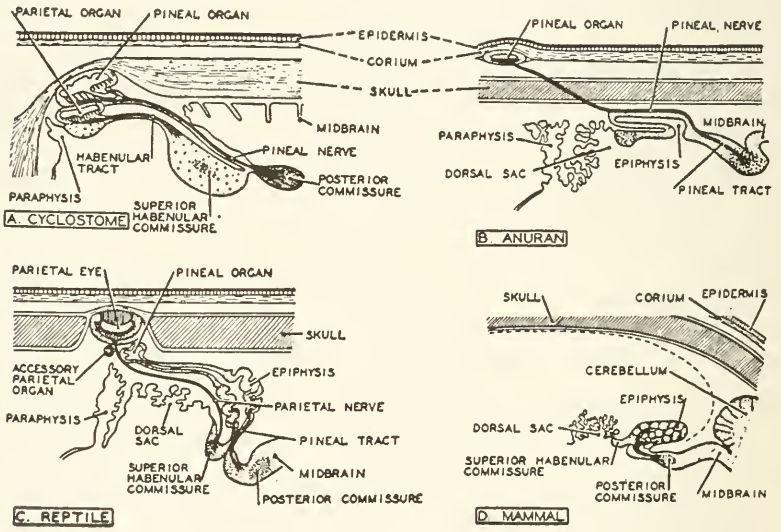

Fig. 1. Diagrams of pineal (epiphysial) and parapineal (parietal) organs in the midsagittal plane. (From Neal and Rand.)

In order to understand the significance of the parietal foramen and its variations, without direct knowledge of the related organ, paleontologists must necessarily have recourse to study of the conditions in the extant Lacertilia. Lizards are the only group in which the variable relations between the parietal organ and the parietal foramen can be observed.

There are two other extant types whose pineal apparatus includes parietal eyes with access to them of light through the skull roof. In the lowest of living vertebrates, the lampreys, both the pineal and the parapineal organs have elements of an

eye as well as of a gland. The petromyzontid condition is important to paleontologists in evolutionary speculations, but not in the study of paleo-anatomical detail; the lamprey skull is not ossified but consists of cartilage and connective tissue, that is, of tissues almost never found in a fossilized state. The other extant type with a parietal eye is another reptile, *Sphenodon.* But this last of the Rhynchocephalia survives into the Present with only one species. In contrast, the Lacertilia still flourish with several thousand species, of which numerous specimens from almost a hundred species have been used for studies of the pineal complex.

In the course of preparing a survey of the parietal foramen through the ages, I have become acquainted with much of the literature on the pineal apparatus. A recent review lists 1762 papers (Kitay and Altschule, 1954, pp. 107-271). Extensive surveys from Agnatha to man have been made, respectively, by a zoologist-librarian (Studnicka, 1905), a neurologist and a physician (Tilney and Warren, 1919), an embryologist and a surgeon (Gladstone and Wakeley, 1940). "The solution of the pineal riddle"[1] (Bargmann, 1943, p. 311) has been attempted, further, by endocrinologists and pathologists, physiologists and psychiatrists, anatomists and comparative anatomists. While paleontology has contributed not more than occasional observations and some speculations, neontologists have freely drawn conclusions as to the state of parietal organs in various stages of vertebrate history. Their concepts were, of course, based on the pineal complex in the scale of living vertebrates, its embryogenesis, its manifest involution in individual life, and sometimes also on fossils. "A relatively or actually large foramen in the skulls of the more ancient types of fossils and the tendency for it to lessen in size or disappear in the more recent types and living species indicate that the pineal organ itself was more highly evolved in the more ancient and primitive types, and has become vestigial in the living representatives of these types" (Gladstone and Wakeley, 1940, pp. 236-237). Paleontologists, so far as I know, have never even protested that the types so connected to demonstrate this supposed trend are not ancestors and descendants. They have actually been discouraged from participating in the discussion: they have been warned that, in

[1] Foreign language quotations are translated.

the case of parietal eyes, fossil specimens cannot reveal the condition, or even the presence of the vanished organ.

The first purpose of the present paper is to reject this warning. Those pineal organs in which the gland potentiality was dominant have vanished without trace in fossils; but the condition in living lizards shows that reptilian fossils *do* provide a reasonably reliable record of those organs in the pineal complex in which the sense organ character was dominant.

OPINIONS

In the literature on the pineal complex, various statements of a general nature are repeated over and over again. One reason for this appears to lie in the fact that pineal problems have attracted students in so many fields. For example, a zoologist (Stadtmüller, 1936, p. 597) perpetuates the opinion of a neo- and paleo-zoologist (Döderlein, 1890, p. 595) who, in a general description of the tetrapod skull, wrote as follows: "A parietal foramen is present only in the more primitive forms. It is highly improbable that this should have corresponded to an unpaired parietal eye." It is true that the term "parietal foramen" has been applied to mid-dorsal openings in the skull of certain Eocene and Recent teleosts, fishes which indeed lack dorsal visual organs; but these median gaps actually are fontanelles. The view that pineal organs and foramina in archaic fishes had no visual function probably goes back to Dean's homologizing the mid-dorsal foramen of placoderms with one of the fontanelles of siluroids (1891; 1895, pp. 55-56). The tiny "open or overgrown hole," which was first discovered but not named by Wolterstorff (1886, p. 21) in some but not all fronto-parietal bone specimens of a Miocene frog, has now been found in a total of three Recent anuran genera (Griffiths, 1954). This opening is invariably called a parietal foramen; it is, however, a microscopic, oblique canal containing the vessel and nerve of the mysterious pineal, or pineal+parapineal, extracranial frontal organ of the Anura (Fig. 1 *B*). Irregular venous foramina in mammalian parietal bones are likewise called parietal foramina. But all these structures—in teleosts, anurans, and mammals—are easily distinguished from the foramen associated with a

parietal eye. This quite distinctive feature last occurred, in Pisces, in the Carboniferous period; in Amphibia, in the Triassic. Among the extant vertebrates with an ossified cranial roof, the genuine parietal foramen is found only in the tuatara and in lizards, that is, only in animals that have a photoreceptive parapineal organ. If one doubts that this association existed also in extinct vertebrates, one may as well doubt that the orbits of fossil skulls contained eyes.

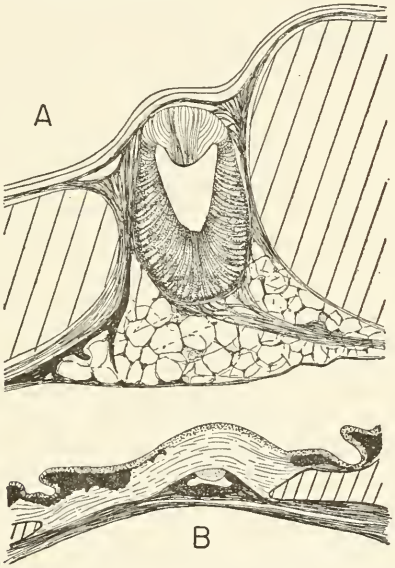

Fig. 2. *A,* Parietal eye filling parietal foramen (*Anolis* sp., after Spencer; enlargement not known). *B,* Parietal eye in exceptionally wide foramen (*Agama sanguinolenta,* after Schmidt; x 30).

Functions other than visual have been attributed to the parietal organ of lizards for almost a century. It has also been regarded as an inactive rudiment of a larger organ which, in Reptilia of the Past, had an unknown, presumably sensory function, related to conditions not occurring in the Present. The majority of students, however, have realized that its structure clearly points to one function: photosensitivity. Thermosensitivity may be associated with this, and granules apparently secretory in nature have been found in the organ; but, mainly, the

parietal organ is a photoreceptor. The names of lateral eye elements are used in its description. Wrapped in loose, vascularized connective and some mucous tissue ("sclera"), the parietal vesicle lies below or in the parietal foramen, above which a spot of skin may be conspicuously light in color ("cornea"). When the organ is fully developed and has not undergone involution, its distal wall is in great part translucent ("lens"). Its equator and proximal wall ("retina") contain supporting cells with light-absorbent pigment, sensory cells, and ganglion cells whose centripetal processes form the parietal nerve.

Opinions long proven to be erroneous keep reappearing because the relevant papers are published in journals serving fields of science too varied to be noticed by workers in any one field. Recent authors are victims of this situation when they write: "There is no experimental proof that parietal eyes of lizards or *Sphenodon* can perceive light rays" (Stigler, 1950, p. 316), or: "Clearly it cannot be an organ of sight; and equally clearly it cannot be an eye in the true sense" (Burton, 1954). Images, of course, cannot be perceived by the parietal vesicle; and it is true that experiments with only negative results were reported in a 1911 paper quoted by Stigler and in a 1907 paper quoted by Burton. But in later work reactions to light and darkness of the lizard parietal organ have been demonstrated by several methods (shift of pigment, e.g., Trost, 1953, p. 202; change in oxygen consumption, Clausen and Mofshin, 1939). Sufficient proof now exists that in some lizards the parietal eye helps to distinguish light and dark.

Actually it is to be expected that in some individuals the parietal organ is found to function as a photoreceptor while in other individuals light rays concentrated on the parietal skin spot fail to produce any reaction of the animal. To explain the variable results of experiments one has only to note the variability of structure reported by the histologists. The parietal nerve, for example, is clearly seen in the embryo and very young, but has rarely been found in adult lizards (discussed by Bargmann, 1943, p. 455). Absence of the cranial opening is commonly regarded as a specific or generic character; but I have come to realize that the parietal foramen can close during individual life, a rough macula of bone being built up in its place (Fig. 4*D*).

Even Spencer, the first to compare parietal eye preparations from many (28) lacertilian species, observed that in every specimen there is at least some one feature in which the eye or the parietal skin spot is less perfect than in other specimens. He concluded "that the pineal eye in Lacertilia is a rudimentary structure—that at the present time it is not so highly developed as it must have been at some previous period when fully functional" (1886, p. 216). This idea found much support, authors citing very large parietal foramina in some reptiles of the Past.

One must realize that, in contrast to the foramen, the structure of the parietal organ is revealed only in microscopic sections. Students of such preparations have not in general been concerned with the size of the organ. I found only the following data in the literature. Spencer was amazed to find the axis of the eye 0.4 mm. long both in a 2-foot long *Sphenodon* and in a 6-foot long *Varanus* (1886, p. 183). Longitudinal and transverse diameters varied from 0.18 to 0.20 mm. and from 0.06 to 0.07 mm. in the *Anniella* specimens of Coe and Kunkel (1906, p. 393); mediodorsal skull length is about 8 mm., and length of the animals 105 to 152 mm. from snout to cloaca, plus a post-cloacal portion varying from 16 to 75 mm. (*ibid.*, p. 351). Slightly larger parietal eye diameters in *Phrynosoma* have been expressed in microns: 258μ and 171μ (Ritter, 1891, p. 212). In short, the diameters of measured lizard parietal eyes were fractions of millimeters.

In the vast majority of lizards the foramen—correspondingly, it appears—ranges from pinpoint size to diameters of about 1 mm. Diameters "of considerable size", namely 2.2 and 2.6 mm., were noted by Schmidt (1909, p. 373) in two agamid individuals. Also among the dozens of lizard skulls I studied, diameters of more than 1 mm. are rare. I found 4 Agamidae and 3 Iguanidae with diameters of 1.1 to 2.0 mm.; and the largest, by far, in the MCZ Department of Herpetology is the parietal foramen of the lizard giant, *Varanus komodoensis,* which is 3 mm. long and 2 mm. broad (the skull, 190 mm. long). On the other hand, among extinct Reptilia one can encounter a parietal foramen as much as 50 mm. in length and 20 mm. in breadth—in a Jurassic plesiosaur, *Pliosaurus,* whose skull, lacking tip of muzzle, is 1100 mm. long (Linder, 1913, p. 394).

Certainly one must conclude that an extinct reptile such as

this plesiosaur had a larger parietal eye than have the Lacertilia. On the other hand, there are no data of any kind to support the idea that in the Past parietal eyes were different, were more elaborate in structure, than they are in the Present. If there had existed, for example, auxiliary structures such as muscles and extrinsic nerves to move the parietal eye, their traces should be found in the walls of parietal foramina of at least the type shown

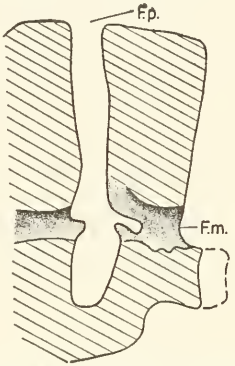

Fig. 3. Tapinocephaloid. Median section through back part of skull. *F.m.*, foramen magnum, *F.p.*, parietal foramen. (After Haughton 1918; x 1/6).

in Figure 3. Further, the ontogenesis of the lacertilian pineal complex has been thoroughly investigated, over the past 70 years, by a great number of students, in innumerable embryos of many species. Although the process is by no means always the same in every detail, never has anything been observed which could be interpreted as indicating an originally more complicated structure of the parietal eye.

In the concept that in fossil reptiles with a large parietal foramen the organ had great photoreceptive power, it need not be assumed that the structure was different from that in lizards. Size obviously has no necessary relation to function in the lateral eyes of vertebrates; the big eyes of a cow see less well, the tiny eyes of an eagle see far better than human eyes. The parietal photoreceptor, however, in contrast to the highly differentiated lateral eye, has no provisions to control the access of light rays. The amount of light received by its retina must depend only on the size of the lens, and thus of the vesicle. The tacit assumption

is reasonable that the larger a parietal organ is, the more light stimuli it will absorb and transmit.

Although the volume of the parietal vesicle must in some lizards be several times that in others, one cannot well imagine that among the Recent Lacertilia photosensitive capacity is very much greater in larger than in smaller parietal eyes. It can hardly matter much whether in these minor aids to the major photoreceptors (later eyes and skin) the lens diameter is a greater or lesser fraction or, possibly, all of 1 mm. Far greater lenses, however, must be assumed to have existed in several extinct branches of the Reptilia. It is with regard to these that the questions of parietal eye size become interesting.

In consequence, great importance must be attributed to the widespread opinion according to which a large parietal foramen does not necessarily reflect the presence of a large parietal organ. It was formulated as follows by Camp (1923, p. 395). *"The size of the foramen has no relation to the size of the eye in the latter group* [Lacertidae]. *Those who would relate functional significance of the eye with size of the foramen in fossil forms should note this."*

This challenge to paleontology has never been met. It has not even been discussed. Yet it can be successfully combatted—with, of course, the material of neontology.

Camp's studies of actual specimens, like my own, were not of the organ but of skulls. His conclusion as to the absence of size relations between organ and foramen was drawn from zoological papers that he quotes. During my more extensive perusal of the literature I came to recognize this opinion as one of the many generalizations about the pineal apparatus that have acquired seeming overall validity merely by being repeated for decades.

FORAMEN-EYE RELATIONS IN LIZARDS

Literary data. The papers dealing specially with parietal eyes contain in their texts very little information about size relations between eye and foramen. With the exception mainly of Studnicka (1905) and Schmidt (1909), those who described the organ did not mention the foramen—although bony foramen margins occasionally appear in one or both upper corners of their figured microscopic preparations.

The consequences are evident whenever a general statement has seemed necessary, such as in the big monographs mentioned in the introduction. In one of them the authors agree with Camp and others: "The size of the foramen differs and bears no direct relation to the size of the parietal eye" (Tilney and Warren, 1919, p. 131). Another survey, in a chapter entitled "The Parietal Foramen in Reptiles", says of the parietal eye that "as a rule . . . its diameter is about one-third the diameter of the foramen" (Gladstone and Wakeley, 1940, p. 270). No references are given. That 1:3 proportion has indeed been reported—namely, in one *Phrynosoma* individual. While not stressed by the describer of the specimen (Ritter, 1891), the condition was mentioned by Studnicka in his monograph—but mentioned as a case of quite exceptional discrepancy between organ and foramen (1905, p. 160).

In *Phrynosoma,* Studnicka's own specimen also showed "an extraordinarily broad parietal foramen. It is a big gap in the bony skull roof, about four times as broad as the parietal eye" (1905, p. 181). A foramen with an abnormally large transverse diameter seems quite likely to occur when the opening lies in the crossing of the frontoparietal and mediosagittal sutures in a thin skull, particularly in a young lizard. It can then even have the shape of a T. In such a case, the transverse bar of the T is an unclosed middle section of the frontoparietal suture, the longitudinal bar a gap either between the two frontal bones (Engelbrecht, 1951, fig. 10) or between the two parietal bones: a parietal foramen not fully framed. In none of the fossil reptiles I know is there a particularly broad parietal foramen; it is either a longitudinal oval or a circle, very rarely a little broader than long. Should a T-shaped opening be found in a fossil, it would certainly be recognized as a fontanelle rather than a foramen. There could be no misunderstanding the fact (Engelbrecht, 1951, p. 21) that only the middle section is related to the parietal organ.

The concept of independent size variation of the parietal organ and its foramen is, admittedly, a generalization, based on data reported in special studies of the organ. The basis is, I have found, psychological rather than factual.

When Spencer (1886, p. 215) wrote that in his specimens of *Lacerta ocellata* and *Cyclodus* "the eye is placed within the

parietal foramen, fitting it closely", this was an incidental observation in a discussion of positions of the parietal eye. Schmidt was the only author who, with a large amount of material, paid attention to and discussed size proportions of eye and foramen. Understandably, he noted and reported the conspicuous and the exceptional conditions—as did Studnicka in his survey. Only the following data are mentioned in Schmidt's text (1909).

Much as in a previously figured *Anolis,* in which "the parietal eye occupies the entire foramen space in thick bone" (p. 374; our Fig. 2*A*), the foramen was only slightly wider than the eye in one of Schmidt's *Anolis cristellatus* specimens, but "approximately double the size of the eye" in another specimen (p. 381). In one of Schmidt's other Iguanidae, a specimen of *Hoplurus,* the diameter of the foramen was approximately 6 times that of the eye (*ibid.*). In some but not all specimens of *Agama* the diameter of the foramen was "a multiple" of the eye diameter. It was because the foramen was almost filled by the eye in the *Lacerta ocellata* specimens of other authors that Schmidt mentioned one case of a foramen "more than five times as large as the parietal eye" (p. 392). And it was in connection with this case that Schmidt quoted, and gave enduring character to the opinion laid down, without any example, by Carrière (1889, p. 146): "There is no relation at all between the size of the parietal foramen and the size and development [Ausbildung] of the parietal organ, nor between the size of the foramen and the position of the organ. . . . Bone structure in this case allows no conclusions as to the soft organ we regard as related. The common conclusion, based primarily upon the larger size particularly of a fossil foramen, that the organ was on a higher level of development, is inadmissible."

While this statement, being carried on and on in the literature, must have discouraged paleontologists, certain observations of Schmidt himself teach the student dealing solely with bones how he can recognize cases in which the foramen may be considerably larger than was the organ.

In the *Hoplurus* specimen, Schmidt reports, the parietal bone tapers to a very thin lamina as it approaches the foramen. In all the *Agama* specimens with a wide foramen, the parietal bones were thin plates, thinning further towards the foramen (Fig.

2*B*). The *Lacerta ocellata* specimens which Schmidt found described in the literature had parietal bones far thicker than the specimen in which he found the wider gap. The numerous specimens of 40 lizard species which he studied, taken together, convinced Schmidt (p. 374) that the parietal foramen is small, more or less fitting the organ, in thick bone. A foramen much wider than the organ occurs in bone which is thin and which, further, tapers toward the foramen. "It seems plausible that in a thick bone the tendency and capacity to lessen or close an opening are greater than in a thin bone."

One wonders whether the latter condition (thin bone: wide foramen) is a phase preceding the former (thicker bone: close-fitting foramen) in ontogeny. Apparently the question has never been raised as to whether in the Lacertilia a wide parietal foramen is a character of very young individuals. In descriptions of post-embryonic specimens, body length is hardly ever given, and individual age never. Probably, as little was known of the age of these Recent specimens as is the case of all fossil individuals. Hanitsch (1889) did compare two age stages; but his specimens were, besides one adult, two newborn *Anguis* whose parietal bones were still unossified. Significantly, however, in a nearly mature embryo of *Lacerta* the parietal foramen was described as "a very large pentagonal fontanelle" (Parker, 1880, p. 630).

Among the specimens cited above as examples of absolute size of the parietal organ is a *Phrynosoma* in which the organ diameters were 0.26 and 0.17 mm. Two other *Phrynosoma* specimens were cited among those with foramina much wider—3 x and 4 x wider—than the organ. However, in one of the two MCZ *Phrynosoma* skulls, both 15 mm. long dorsomedially, I could not find the foramen with a magnifying glass, and in the other the foramen is a minute circle, just visible to the naked eye: it is not larger than the organ whose diameters were measured. The conclusion forcibly presents itself that in the two individuals with great size discrepancies between organ and foramen the parietal bone was not fully ossified. Presumably they were younger than either the individual in which the organ was measured or those represented by the MCZ skulls. (Perhaps very young heads were purposely chosen for sectioning in preference

to heads containing such thickened, knobby, and strongly spined skulls.)

Studying the skulls alone can not, of course, answer the question as to whether the relation between the soft organ and the skull foramen is different in the very young from that in the adult. Study of the MCZ collection of lizard skulls, all of them well ossified, showed only that there is much individual variation in foramen size, and that fortification of the foramen

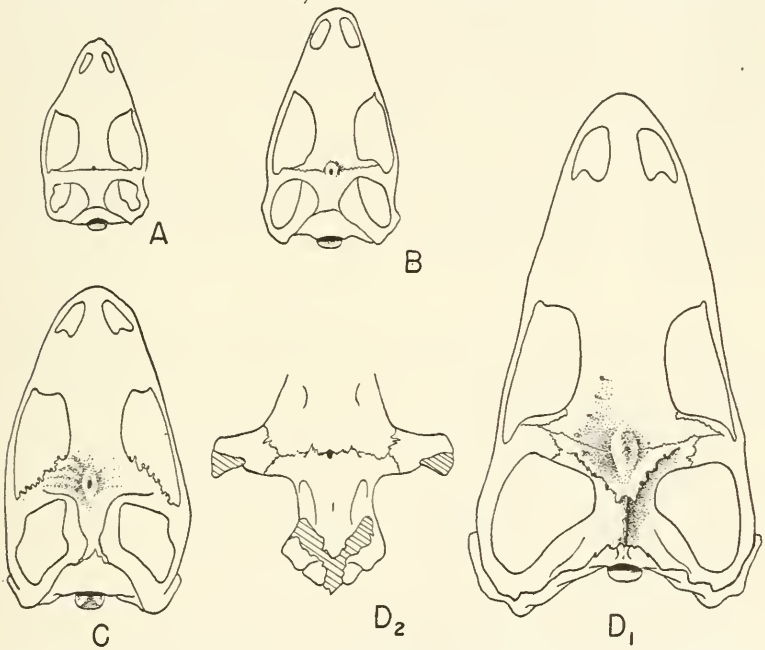

Fig. 4. *Iguana iguana* (*A, C*) and *Iguana rhinolopha* (*B, D*). D_2, Ventral view of cranial roof, showing remnant of dorsally closed parietal foramen. x about 2/3.

by a ring of dense bone (Fig. 4) develops at different ages in different individuals; and it suggested that closure of the foramen (Fig. 4*D*) occurs late in individual life.

It may well be because specimens of fossil reptiles are not, in general, those of very young individuals that I know of no fossil parietal foramen with tapering margins. Many types of

extinct reptiles have, on the contrary, the foramen margins raised and buttressed, as have some lizards. In several kinds of mammal-like reptiles, such fortification developed into "a sort of cyclopean periscope" (Gregory, 1926, p. 186) rising above the general level of the parietal region—a large perforated boss (e.g., *Moschops; ibid.,* pl. XV) or a chimney-like structure (*Hipposaurus;* Haughton, 1929, fig. 20). A strikingly large parietal opening is often found in very thick bone—indeed, a canal rather than a foramen (Fig. 3). Thick bone, be it noted, is a condition in which, according to Schmidt's considerable material of Lacertilia, major size discrepancies between parietal foramen and organ do not occur.

While occasionally highlighting cases in which the parietal foramen was found strikingly larger than the organ, the descriptions of the parietal eye in Lacertilia have nowhere answered the question of what, if any, are its normal size relations to the foramen.

Figured data. Not the texts of the parietal eye studies but their illustrations constitute a record of relations between the organ and the parietal foramen.

In all suitable figures that I could find, I have measured the maximum diameter of the eye (without the surrounding "sclera") and the minimum diameter of the foramen. The ratios of eye diameter to foramen diameter are listed in the table (p. 00).

It is unfortunate that these ratios must be interpreted without regard to age factors, as the latter are unknown. Moreover, the list is rather short. The big surveys by their rich illustration suggest that the literature they summarize must contain many figures well-suited to the purpose, showing in section not only the eye but also both sides of the foramen. Actually, a 1940 figure for example is likely to be a copy, from Studnicka 1905, of a 19th century figure. The data I brought together were found in figures published by the following authors: Boveri (B), de Graaf (G), Hanitsch (H), Leydig (L), Owsiannikow (O), Schmidt (S), Spencer (Sp), and Studnicka (St).

TABLE OF RATIOS

BETWEEN PARIETAL EYE (=1) AND PARIETAL FORAMEN

Seps (L)	0.4	*Lacerta* (L)	1.4
Chamaeleo (S)	0.5	*Lacerta* (St)	1.4
Chamaeleo (S)	0.7	*Lacerta* (Sp)	1.5
Anguis (G)	0.8	*Varanus* (Sp)	1.5
Seps (Sp)	0.8	*Chamaeleo* (Sp)	1.5
Lacerta (L)	0.8	*Lacerta* (L)	1.6
Lacerta (L)	0.8	*Chamaeleo* (Sp)	1.7
Varanus (Sp)	1.0	*Varanus* (Sp)	1.7
Mabuia (S)	1.0	*Pseudopus* (St)	1.8
Lacerta (L)	1.1	*Varanus* (B)	1.8
Lacerta (L)	1.1		
Lacerta (L)	1.1		
Anolis (Sp)	1.1	*Lacerta* (Sp)	2.1
Eumeces (S)	1.1	*Calotes* (Sp)	2.1
Lacerta (O)	1.2	*Leiodera* (Sp)	2.2
Chalcides (S)	1.2	*Moloch* (Sp)	2.3
Pseudopus (St)	1.3		
Lacerta (L)	1.3		
Agama (B)	1.3		
Chamaeleo (B)	1.3	*Agama* (S)	3.2
Anguis (H)	1.4	*Plica* (Sp)	5.8

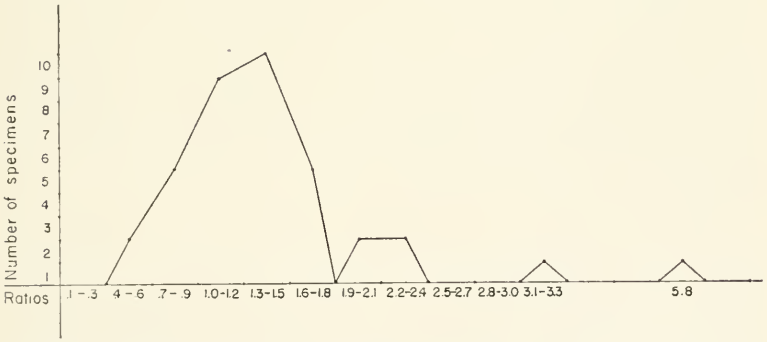

Fig. 5. Distribution of diameter ratios between parietal eye and foramen; data from table.

The illustrations in which I measured diameters of parietal eye and foramen represent 37 individuals. The table, and the graph illustrating the table (Fig. 5), show that the ratios fall

into three groups. The small gap between the first and second group is, however, probably not a genuine separation but merely due to the paucity of specimens.

By far the largest group is the first. Thirty-one ratios form a continuous series in which the foramen diameter varies from about one-half[1] to one and four-fifths times the diameter of the eye. One or both the *Anolis* specimens mentioned by Schmidt also belong in this group. The majority of the specimens (19) are in the 1:1 to 1:1.5 range. This is a span of size relations to be expected between an organ and an orifice formed by the more or less remote influence of the organ to keep it open and by the tendency of bone growth to close it. One must remember that for capacity function of the parietal eye the foramen need not be much larger than the "lens"; that there is great variation in the thickness of the "scleral" tissue outside the eye proper, as also in the amount of its blood capillaries; and that the eye is never directly in touch with the foramen margins. One also has to consider a feature of the material on which the table is based. When the direction of a figured section is mentioned at all in the caption, it is identified as medio-sagittal, i.e., longitudinal. As the foramen is either circular or a longitudinal oval or slit, I must have, in general, measured the longest diameter of the foramen, while transversely the eye: foramen ratio was presumably smaller.

In the second group, in 4 specimens, the foramen diameter is slightly more than twice the diameter of the eye. This brings to 35, out of 37, the cases which, to me at least, demonstrate that, although the two related structures are not in contact, there does exist a definite if variable size relationship between foramen and eye.

Only 2 specimens are in the third group, that with foramina 3 to 6 times as long as the eyes. This, however, is the group to which must be added cases described in the literature, quoted above: 2 *Phrynosoma* (x3, x4), 1 *Hoplurus* (x6), 1 Lacerta (more than 5 x) and possibly some of Schmidt's *Agama* specimens ("a multiple"). As such great differences in size were observed in particularly thin skulls, they probably occur in particularly young individuals.

1 The *Chamaeleo* cases are abnormal: the degenerated eye lies above the foramen.

Taking together the evidence of published figures and the data reported in texts, we see that there are 35 cases of what may be taken as normal size relations, against the 6 definite cases of considerable discrepancy which have been so highlighted in the literature as to put in doubt all paleontological research on the pineal complex.

From the structure of the lacertilian parietal organ we have above concluded that it must be a type of photoreceptor whose capacity is proportionate to its size. In my opinion, the size relations between foramen and eye in the extant Lacertilia entitle the paleontologist to conclude that the larger a parietal foramen is in a fossil skull, the larger was the organ it served.

FORAMEN AND SKULL

The size question. What do the authors mean when they write about "small" and about "large" parietal foramina? It is odd that this question should have to be asked, but I have not found it answered in either the neontological or the paleontological literature.

Wettstein, zoologist, stated that *Sphenodon,* "representative of the lowest evolutionary stage among the living reptiles . . . has a relatively large parietal foramen" (1931, pp. 2, 33). This, presumably, is meant to say that a tuatara skull has a larger parietal foramen than a similar-sized skull of other living reptiles. This is indeed the case; the foramen is 3 x 1 mm. both in an MCZ tuatara skull (mediosagittal length 56 mm.) and in Wettstein's specimen (*ibid.*, fig. 37; skull 51 mm.). Among the comparable lizard skulls I measured, the largest foramen is 1 x 1 mm.

Huene, paleontologist, made a survey as to "which stegocephalians and reptiles have a relatively large-sized parietal foramen" (1933, pp. 372-373). He concluded from the distribution of "large" foramina that the parietal eye was a more potent organ in certain underwater conditions than it was, and is, in terrestrial habitats. From this it would seem that by size Huene meant absolute size, and by "relatively large" he meant that the foramen is absolutely larger in one group than in another.

I realized, however, that this interpretation was wrong when I checked on one of Huene's examples—the suborders of the Sauropterygia, an extinct order on which Huene is an expert, and of which I have measured the foramen parietale in numerous skulls (Edinger, MS, in preparation). "In the placodonts that foramen is large, in the nothosaurs smaller, and similar in the plesiosaurs" (Huene, *loc cit.*). But, in e.g. the Middle Triassic, *Placodus* skulls (median length 158 to 200 mm.) have the parietal foramen 10 to 19 mm. long, with breadths from 10 to 14 mm.; and in *Nothosaurus* skulls (125 to about 800 mm. long), length of the foramen ranges from 4 to as much as 23 mm., breadth from 2.5 to 23 mm. Parietal foramina still larger developed later in at least one infraorder of the Plesiosauria. A 50 mm.-long foramen was mentioned above; there have further long been on record another Jurassic *Pliosaurus* (maximum skull length 1160 mm.) with a 40 x 15 mm. foramen (Linder, 1913, p. 394), and a Cretaceous *Brachauchenius* (skull about 800 mm.) with a foramen approximately 40 mm. in length (Williston, 1907, pp. 479, 484). It thus appears that Huene's statements regarding the size of the opening did not imply absolute size but, rather, size relative to skull size.

The fact is that the parietal foramen is a far more conspicuous feature in the center of a short, broad *Placodus* head than in the back part of the slender, elongated head of *Nothosaurus* or a plesiosaur. I believe that this is what most authors have in mind when they call a parietal foramen large or small; they mean the size of the foramen relative to the size of the whole skull. Others apparently intend to say that the foramen they describe is larger or smaller than in some other form whose head, or perhaps whose body is of comparable size. Those few who paid attention to the foramen: organ ratio called "small" a parietal foramen approximately the size of or smaller than the organ, while "large" in such a study means that a foramen is larger than the organ. There has, further, been occasional comment on small size of the parietal foramen as compared with the lateral eye orbits. Still further, some authors must have been thinking merely of absolute size of the parietal foramen.

An answer. Great differences in absolute size of the parietal

organ and hence of the parietal foramen presumably are, we have seen, significant physiologically. But in the comparative anatomy of a group as vast as the Class Reptilia the meaning of absolute size of the foramen differs enormously. We have to compare tiny animals with animals whose body is a hundred or a thousand times larger. Obviously, the size of the parietal organ relative to the size of the body would be not only difficult to calculate but also of dubious value. The same is true of the size of the foramen relative to the skull as a whole. We find the foramen in skulls compactly constructed, and in skulls drawn out into short or long muzzles; but the parietal foramen is a part of the cranium, the "Hirnschädel" of German terminology which, like the brain, is never involved in the process of skull elongation as much as the facial portion ("Kieferschädel").

A meaningful expression of parietal eye size can be found through the fact that this organ, in contrast to the lateral eyes, is entirely a part of the brain. Skulls do not build a separate orbit to lodge the parietal eye. This lies either within the brain chamber or, if in the parietal foramen, in an extension of the brain chamber.

Seeing the parietal eye as one of the brain organs, one is not surprised by the discovery of Spencer quoted above—namely, that this organ can be of the same size in a two-foot long and in a six-foot long reptile. The entire brain, including the extensive olfactory tracts whose length necessarily varies with skull length, was found to be 70 mm. long in a *Python* of about 6.5 m. length, and 40 mm. in a *Python* of about 2.5 m. length (Edinger, 1929, p. 100). The difference in brain-to-body length ratios (1:93 and 1:63, respectively) would be far greater if only the contents of the braincase proper had been measured.

It follows that calling the parietal foramen small in large animals or in large skulls may be as unfortunate as the common usage of calling the brains of elongated heads smaller than the brains in short heads. It is even assumed that the former are less efficient than brains which constitute a large portion of the head. Efficiency of the various brain functions depends, of course, much more on the composition than on the size of the brain, relative or absolute. Greater or lesser relative size, within the brain, of one or more of its components, is in general the

anatomical correlate of greater or lesser importance of the functions they serve.

In consequence, a parietal organ should be regarded as large when it is a relatively large appendage of the brain. Its osteological reflection, the parietal foramen, is large when it is a considerable interruption of the braincase roof, otherwise closed.

In many reptiles an approximate size relation of the parietal organ to the rest of the brain can be shown three-dimensionally by endocasts of the braincase (Fig. 6). This method, however, is not practicable in the Lacertilia and the many other groups whose braincase is not a complete bony capsule.

But even in species whose braincase is incompletely ossified, an index of brain size is available. The occipital area, which lodges the hindbrain, is usually well ossified. Consequently, macerated or fossil skulls in which the foramen parietale is also present include the foramen occipitale magnum. This surrounds the posterior end of the brain. The lumen of the foramen magnum is somewhat larger than but corresponds approximately to a cross section of the medulla oblongata. The relation between bone and medulla is here similar to that between parietal foramen and parietal eye. In both these cranial openings, size differences roughly represent size differences of the related organs. Comparing the diameters of foramen magnum and foramen parietale is a method not as exact as paleoneurology can use in other investigations but preferable, I believe, to the vague methods of comparison hitherto used. I regard as a fortunate circumstance the fact that the brain area whose osseous counterpart we can compare with that of the parietal eye is in the most conservative portion of the brain. The medulla, in contrast to the brain as a whole, is of similar shape in all reptiles; and its thickness varies mainly, or exclusively, with body size.

For the appraisal of parietal organ size by measuring and comparing the diameters of foramen parietale and foramen magnum, an immense amount of material is available in extinct and extant reptilian skulls. However, for large-scale comparisons of the two foramina, paleontology is under more than its usual handicaps. Crushing of course can practically eliminate even the foramen magnum (for example, in all plesiosaurs preserved in slates). A fragment may contain one but not both foramina. The good fossil skulls are held in collections all over the world; de-

scriptions of them rarely list foramen diameters, and figures show but indistinctly that small feature, the parietal foramen.

A few examples will be given here of this means of comparison. We will first reconsider from this viewpoint animals mentioned above in one or another context. We can then examine with this method two of the general evolutionary concepts mentioned which, incidentally, are contradictory (as is typical of the pineal complex literature). Is the size of the parietal organ correlated with the habitat of a reptile? Do large parietal foramina occur only in very ancient and/or very primitive reptiles?

The parietal foramen of *Sphenodon* is larger than in lizards relative to the brain, as expressed by the approximate breadth and height of the medulla oblongata as well as by other standards of comparison. In the two skulls mentioned, in which the parietal foramen is 3 x 1 mm., the foramen magnum is 5 x 5 (MCZ) and 5 x 4 mm. (Wettstein, 1931, fig. 32).

The relatively smaller size of the parietal foramen in Lacertilia may be illustrated by two series of skulls in the MCZ Department of Herpetology. One series consists of 8 *Iguana* skulls with dorsomedian skull lengths from 38 to 100 mm. Nos. I and IV-VII are *I. iguana;* II, III and VIII are *I. rhinolopha* (see Fig. 4). The foramen magnum is 5 x 4 mm. in the smallest, 5 x 5 mm. in the next four, 6 x 6 mm. in a 64 mm.-long skull, but 7 x 7 mm. in a 60 mm.-long and in the largest skull. The parietal foramen measures fractions of 1 mm. in I, IV and VI, and reaches diameters of 1 mm. in II (length even 1.2 mm.), III, V, VII. The foramen is dorsally closed in the 100 mm. skull; its remnant is a ventral circular pit with 1 mm. diameters.[1]

The other series is one of six skulls of *Ctenosaura pectinata*, 55 to 84 mm. long. Breadth of the foramen magnum rises from 5 to 6 mm. and so does height except that, while it is 6 mm. in specimens IV and VI, height is only 5 mm. in V. The parietal foramen is 1 x 1 mm. large only in IV and in VI, the largest skull. Length is 1 mm. also in the smallest specimen, but breadth is less than 1 mm., as are the diameters in the other three specimens.

[1] As the closure phenomenon is apparently not previously noted in lizards, I may add here that it is also shown in a series of eight *Physignathus cocincinus* skulls 36 to 52 mm. long. The parietal foramen, invisible to the naked eye in the smallest, tiny in all others except in one of the five 45 to 47 mm.-long skulls (1 x 0.5 mm.), is closed in the largest specimen.

The parietal foramen of the giant, *Varanus komodoensis,* so conspicuously large with diameters of 2 and 3 mm., is similar in relative size to that of some of the smaller lizards; the foramen magnum is 14 mm. broad and 12 mm. high.

If an attempt is made to compare the areas rather than diameters of the two foramina—by the method of multiplying with each other the diameters of the openings—the difference between the rhynchocephalian and the lizards becomes quite striking. The parietal foramen then compares to the foramen magnum as 1:7 and 1:8 in *Sphenodon,* but as 1:28 in *Varanus komodoensis,* and the largest parietal foramina in the *Iguana* and *Ctenosaura* series have ratios of 1:21 and 1:36, respectively.

Briefly, in the lizards I measured, the relatively largest diameters of the parietal foramen are only about one-fifth of the diameters of the foramen magnum; in most specimens they are far less. This is the osteological expression of a parietal eye so small that its existence remained unknown for many decades of research on lizard brains.

Application to fossils. Much larger than in any of the Recent Reptilia was the parietal foramen in specimens of the two sauropterygian genera discussed above. There are late Middle Triassic (Upper Muschelkalk) skulls both of *Placodus* and of *Nothosaurus* in which the foramen parietale is almost as large as the foramen magnum. Before this phase, however, parietal foramen diameters in Lower Muschelkalk *Nothosaurus* averaged only about half those of the foramen magnum; and they seem to have shrunk to about one-third in an Upper Triassic *Nothosaurus.* In the placodonts, the foramen ultimately closed (*Henodus,* Upper Triassic; Edinger, MS. in preparation). Similarly, the foramen had disappeared in the last of the plesiosaurs (at least *Hydrotherosaurus,* late Upper Cretaceous; Welles, 1943, p. 133).

The Placodontia and *Nothosaurus* were semi-aquatic seashore dwellers at the times when their parietal eyes were small and when they were large. It is really not possible to correlate evolution of a large parietal eye with the environment of the animals in which it developed. The history of this structure in placodonts and *Nothosaurus* constitutes but two examples of a phenomenon

which occurred repeatedly in the history of the reptiles. The parietal foramen was enlarged for some time in several branches of the Reptilia, in different habitats, in different periods of earth history.

The story of *Nothosaurus* may, further, serve as one of the actual records which do not fit into the theory that the parietal foramen is larger in primitive than in progressive forms. In this long-lived genus, neither the evolutionary enlargement nor the reduction of the parietal eye was paralleled by any noticeable change in other structures, except that some of the Upper Muschelkalk individuals were very large animals.

When it is said that the genuine foramen parietale occurs only in primitive vertebrates, this is true in so far as neither foramen nor eye are left in birds and mammals. On the other hand, the statements are unacceptable which assert that among those vertebrate groups in which the foramen occurs it is present, or it is large, only in primitive forms. Such assertions do not agree with the record. The vertebrates with parietal foramina are extinct Agnatha, Pisces, and Amphibia, and both extinct and extant Reptilia. I have not yet found a large parietal foramen in a fish; among amphibians, the foramen appears to be large in those labyrinthodont skulls which represent young individuals —but my studies are far from concluded. At present it seems to me that parietal foramina of strikingly large relative size occurred, in gnathostomes, only among Reptilia. Apparently the related ancient photoreceptor came to play a larger role in this class than in the other classes. This view finds support, I believe, in differences between the dorsal eyes of living vertebrates, that is, of lampreys and of reptiles (Fig. 1 *A* and *C*). Only in the reptiles is the ocular structure perfected; only the reptilian parietal eye has a distinct, clear lens.

The various extinct Reptilia in which the parietal eye became large cannot all be regarded as primitive. Permian Therapsida, mammal-like reptiles of the suborders Theriodontia and Dinocephalia were mentioned above as having the parietal opening as a wide canal through a thick skull roof (Fig. 3), or having it strongly buttressed by a superstructure of the parietal bone. In the parietal cone of *Delphinognathus conocephalus*, Seeley found a circular parietal foramen "nearly 2 cm. in diameter"; the foramen magnum "appears to have been not more than 2.7

cm. high by 1.3 cm. wide" (1892, pp. 469, 471). A certain importance of the parietal eye in some kinds of therapsids is also demonstrated by the endocranial cast of a later, early Triassic representative of still another suborder, Dicynodontia. In a 141 mm.-long skull of *Lystrosaurus* (Fig. 6*A*), the parietal foramen does not appear to be particularly large. In the brain (Fig. 6*B*), the parietal organ must have been an appendage of considerable size. The channel it produced in the skull is 18 mm. high caudally where it joins the midbrain chamber. On the

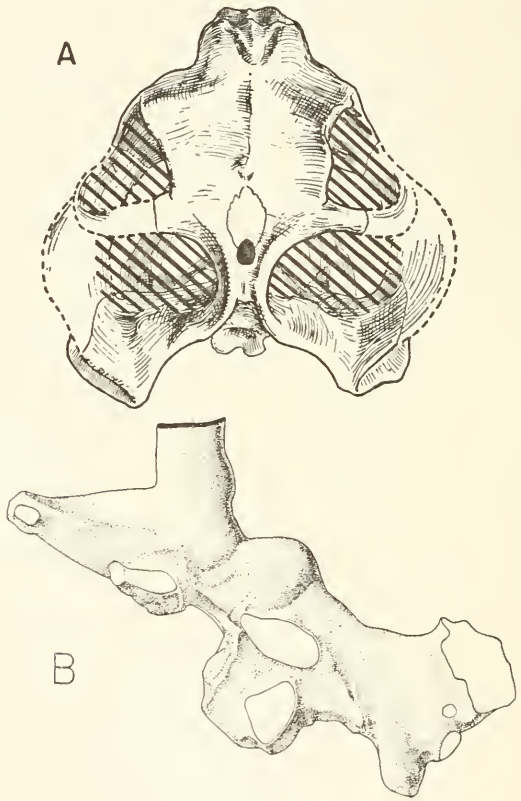

Fig. 6. *Lystrosaurus* sp. *A*, Skull in dorsal view, from Huene 1931; x 1/3. *B*, Its endocranial cast in left side view, M.C.Z. 2124 (duplicate of specimen in Geol.-paläont. Inst. d. Univ. Tübingen; x 1).

outer skull surface the diameters of the opening (9 x 7 mm.) are about half those of the foramen magnum (18 x 13 mm.); but below that, the cast has revealed a 10 x 10 mm. swelling which presumably indicates the position of the parietal eye. As apparently everywhere among the Reptilia when the parietal foramen is known in more than one individual, its variability can be seen in *Lystrosaurus*. In a 171 mm.-long skull, the parietal canal is 17 mm. deep, and its diameters on the surface are 10 and 7 mm., much as in our figured specimen; but the diameters of the foramen magnum, 17 and 23 mm., are more than twice those of the foramen parietale in this larger skull (van Hoepen, 1913, pp. 25, 34). To judge from Brink's figures (1951, 3D and E), the parietal foramen was still smaller, relative to the foramen magnum, in the largest of complete *Lystrosaurus* skulls.[1]

The Therapsida are a reptilian order greatly specialized in the direction of mammals. It contains many forms in which the parietal foramen was very small, and the foramen was lost before the therapsids gave rise to the new class. But in this order there also developed at least some individuals in which the parietal eye was half to fully as large in section as the medulla oblongata.

The most primitive reptiles are included in the order Cotylosauria. According to the general concept of parietal eye devolution, the early cotylosaurs should have the largest parietal foramina among the Reptilia.

A paragon, in the literature, of parietal foramina "exceptionally large" (Gregory, 1951, p. 338), is that of the early Permian cotylosaur *Diadectes*. It is indeed huge as seen in the short and massive skulls, a perpendicular tunnel through an extremely thick skull table. Less impressive is its endocast, seen as a dorsal extension of an endocast of a cranial cavity (Gregory, 1951, figs. 12. 13. A1). As I have reason to suspect that this endocranial cast is not that of one specimen but a composite which Cope took from several cranial fragments, the size of the parietal organ is better appraised by the method used above. Among the *Diadectes* specimens in the American Museum of Natural History, the often-figured, undistorted skull No. 4839 contains

1 *Postscript.* Six *Lystrosaurus* skulls were measured in the paleontological collection of Bavaria and in the British Museum (Nat. Hist.). The foramen magnum diameters are in one case more than three times, in three cases more than twice, and in two cases less than twice those of the foramen parietale.

the foramen magnum as well as the foramen parietale. The former is 17 mm. high and 19 mm. broad. The latter is practically the same size: 16 mm. long and 20 mm. broad (the respective "areas" being 323 and 320 mm.^{2}). A parietal foramen far larger (at least in an absolute sense) is seen in the *Diadectes* fragment AMNH 4352, the partial roof of a skull which apparently was but little larger than No. 4839, and also in the excellent natural (stone-) mould of its ventral side (Gregory, 1951, figs. 12.13. A 2 and A3). While in other specimens the parietal foramen is more or less circular, in this specimen it is

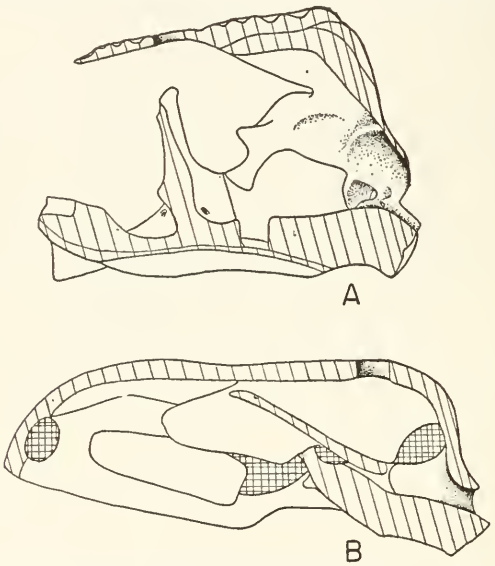

Fig. 7. Right halves of sectioned cotylosaur skulls. *A, Captorhinus,* after Price; x 3-1/3. *B, Diadectes,* after Gregory; x 1/3.

15 mm. broad and as much as 28 mm. long. Thus some *Diadectes* may have had a parietal organ larger, relatively, than e.g. *Placodus.* To judge from figures in the literature, some later diadectomorphs indeed had a parietal foramen larger than the foramen magnum (e.g. *Pareiasaurus,* Boonstra, 1930, figs. 1-2). These later Diadectomorpha, *nota bene,* were among the types more advanced than *Diadectes;* and *Diadectes* itself was not a truly primitive but a rather large and in several respects a specialized cotylosaur.

It is the other, generally more primitive branch of the Cotylosauria, the Captorhinomorpha, which "may lie close to the stem of the reptiles, if, indeed ,the stem reptile itself was not a member of it" (Romer, 1945, p. 173).

Figure 7 serves to compare L. I. Price's (1935) reconstruction of a medio-sagitally sectioned *Captorhinus* braincase, a careful combination of his findings in six specimens, and W. K. Gregory's (1951) similar reconstruction of *Diadectes,* based on the AMNH material. The figure shows that the length of the foramen parietale was much less in the primitive than in the specialized cotylosaur, relative to the height of the foramen magnum. It is true that the foramen magnum is so high in *Captorhinus* that surely not its entire height was occupied by the medulla; its breadth, however, is also greater than the diameters of the parietal foramen, which is circular. In *Protorothyris, Romeria* and other earlier and more primitive captorhinoids, the relative sizes of foramen parietale and foramen magnum appear to be essentially the same as in *Captorhinus,* according to Mr. John B. Clark, who is studying this group. He further informs me that the occiput is generally distorted so that his conclusion is in part based on observations of the braincase as a whole and its relationship to the whole skull, where there is a very strong resemblance to *Captorhinus.*

In *Seymouria,* primitive in combining amphibian and reptilian characters, White (1939, p. 333) described the parietal foramen as shaped like an inverted tunnel, its diameter on the ventral surface of the bone about one and one-half times that on the dorsal surface; reconstructing the braincase on the basis of several specimens, White shows (his fig. 10) the external parietal orifice about one-third as long as the foramen magnum is high.

Thus in at least some of the truly primitive Reptilia the parietal foramen was relatively smaller than in various progressive and in later forms. It was, however, far larger than it is in any surviving reptile.

SUMMARY

It has been claimed that paleontology is unable to contribute reliable data to the evolutionary history of the pineal complex,

although it was in the Paleozoic and Mesozoic eras that numerous types of vertebrates had the parietal foramen. In modern times, this foramen occurs only in Lacertilia and the tuatara, and it is invariably associated with a parapineal photoreceptive organ, the parietal eye.

The idea that the size of the foramen can not reveal the size of the organ is here rejected. The size proportion between organ and foramen does not vary as much in the Lacertilia as was assumed because a few (possibly juvenile) cases of exceptional discrepancies were repeatedly highlighted in the literature. The conditions found in lizards, rather, give confidence in paleontological study—not, of course, of the entire pineal apparatus, but of the parietal eye. The large parietal foramina in some fossil reptilian skulls are valid evidence as to the one-time presence of parietal eyes far larger than have survived into the Cenozoic era.

The concepts that large parietal foramina and organs developed in a particular habitat, or occurred only in very ancient or primitive Reptilia, are put to a test. They appear to be misconceptions due in great part to the lack of a definition as to how the size of the foramen should be judged. As the organ is a part of the brain, it is suggested that the parietal foramen be compared with another cranial opening, the foramen magnum, corresponding approximately to the circumference of another brain part, the medulla. Whereas the diameters of the foramen magnum are, in lizards, at least five times those of the parietal foramen, parietal foramina relatively far larger were evolved in various other branches of the Reptilia. Examples here given of extinct reptiles with parietal foramina close to the foramen magnum in size include terrestrial Permian, and semi-aquatic Triassic forms.

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A CLASSIFICATION OF THERAPSID REPTILES

by D. M. S. Watson and A. S. Romer

CAMBRIDGE, MASS., U. S. A.
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CONTENTS

	Page
Introduction	38
Order Therapsida	42
Suborder Theriodontia	46
Infraorder Titanosuchia	47
Family Brithopodidae	48
Anteosauridae	49
Jonkeriidae	49
Infraorder Gorgonopsia	51
Family Aelurosauridae	52
Aelurosauropsidae	52
Arctognathidae	53
Arctognathoididae	53
Broomisauridae	54
Burnetiidae	54
Cynariopsidae	54
Galerhinidae	55
Galesuchidae	55
Gorgonognathidae	55
Gorgonopsidae	56
Hipposauridae	56
Inostranceviidae	56
Pachyrhinidae	57
Phthinosuchidae	57
Rubidgeidae	57
Scylacocephalidae	58
Scylacopsidae	59
Scymnognathidae	59
Sycosauridae	60
Gorgonopsians lacking family characteristics	60
Gorgonopsians represented by inadequate material	61
Infraorder Cynodontia	61
Family Procynosuchidae	62
Thrinaxodontidae	63
Cynognathidae	63
Diademodontidae	64
Gomphodontosuchidae	65
Cynodontia incertae sedis	65

Infraorder Ictidosauria 66
Family (unnamed) 66
Tritheledontidae 66
Tritylodontidae 67
Microcleptidae 67
Possible mammals from the "Rhaetic." 67
Infraorder Therocephalia 68
Family Pristerognathidae 68
Trochosuchidae 69
Whaitsiidae 69
Euchambersiidae 71
Incertae sedis 72
Infraorder Bauriamorpha 72
Family Lycideopsidae 73
Ictidosuchidae 73
Nanictidopsidae 74
Silpholestidae 74
Scaloposauridae 74
Ericiolacertidae 75
Bauriidae 75
Incertae sedis 76
Suborder Anomodontia 76
Infraorder Dinocephalia 77
Family Deuterosauridae 77
Moschopidae 78
Tapinocephalidae 78
Infraorder Venyukovioidea 79
Family Venyukoviidae 79
Infraorder Dromasauria 80
Infraorder Dicynodontia 85
Therapsida incertae sedis 86

INTRODUCTION

In 1838 a Scottish engineer, Andrew Geddes Bain, who constructed military roads in South Africa, and was the first to determine the general geology of that region, discovered fossil reptiles in rocks north of Fort Beaufort in the eastern part of the colony of the Cape of Good Hope. These were the first therapsids to be found (unless some of those from the Ural mountains were collected earlier) and were later described by Richard Owen. Bain and his son Thomas, Dr. Atherstone and some of his friends,

and some others made large private collections, most of which ultimately reached the British Museum and were also described by Owen. In 1889 H. G. Seeley, aided by a grant from the Royal Society, made a special expedition in order to collect fossil reptiles in the Karroo. This was the first expedition of such a kind ever to leave England, and the first to go to the Karroo. Since then local collectors and visitors from many universities have sought reptiles there. The vision and enthusiasm of Robert Broom, then in medical practice, led to the collection by him, and by men inspired by him, of immense numbers of fossil skulls, few of which are adequately prepared.

Broom described these materials, founding on them several hundred species, each with a short statement of matters wherein it differed from others, and a figure, or more recently several figures. Other men added — and are still adding — to the collections and to the list of conventionally diagnosed species. Thus there are now some 688 species described from the Karroo. Of these the great bulk are therapsids. The rocks which have yielded this immense number of terrestrial vertebrates cover a period from some point in the Middle Permian to the end of Triassic time, about 45 million years.

The therapsids fall essentially into two groups, plant-eating and animal-eating, the first in effect serving as the food supply of the second series. The first group comprises in fact the only plant-eating terrestrial vertebrates of their time, and with a few exceptions (essentially their ancestors) all fall into the group "Anomodontia," typified by *Dicynodon*. The range in size of anomodonts is very great; adult skulls vary from less than 3 cm. to more than 100 cm. in length. There exist very large numbers, certainly several thousand, of complete but usually unprepared skulls, but skeletons are of the greatest rarity; not many more than a dozen are to be found in the museums of the world. The attempts made up to the present to divide this great mass into genera have not reached far, and evidently their understanding will depend not only on much further preparation, but on a greatly improved precision of stratigraphical knowledge. Nothing is so important at the present time as a detailed study of the stratigraphy.

The remaining therapsids, Gorgonopsia, Theriodontia, etc., are more susceptible to classification, and we felt that for our own

purposes some attempt should be made to draw up a scheme, with short diagnoses, isolating groups of species which could thus be handled in the literature.

The great bulk of the species were described by Robert Broom, a man of genius with a unique visual memory and a critical mind. He recognised some hundreds of therapsids which were not anomodonts. Such a wealth of species is in no way improbable; it should be compared with the number of mammalian species found in the Tertiary of the United States from Upper Eocene to Pleistocene times. What this number may be we do not know, but it must vastly exceed the number of Karroo reptiles. Thus we are inclined to believe that the majority of Broom's species may be well founded.

Both the present authors have handled many Karroo fossils, including a considerable part of the type materials. Thus it seemed that direct comparison of figures would allow us to draw up a classification, which could make no pretence to completeness or even probability, but would at least provide some sort of framework for further studies.

The material to which the following classification applies is comparable in variety and complexity to the Class Mammalia. The classification is therefore designed on the broadest lines, the families, apart from the Gorgonopsia, being wide groups including a range of often very varied forms, for no useful purpose could be served by establishing small, tightly defined ones.

Our experience of considering systematically the whole literature of the therapsids has shown us that the continued description of new species of these reptiles on the level which is now customary is most undesirable. What is wanted is a complete preparation, by the acetic and formic acid techniques, of all the existing type skulls. These should then be fully described, and illustrated by figures representing dorsal and palatal views of the skull, lateral views of skull and lower jaw, an occipital view, and probably a detailed figure of the otic region. The figures should distinguish fractures from genuine margin; restorations of broken outlines (which are often useful) should be made in dotted lines outside the damaged edges. The locality and horizon of the specimen must be stated.

The classification of such very varied groups can only progress when the rocks from which they are derived have been adequately

subdivided into stages, and these mapped. The good exposures usual in the Karroo make such mapping easy (in a technical sense) though it involves time and much walking. Such work is by far the most urgent requirement of students of these reptiles, and should have complete priority over the description of any more new species.

Miss Townend made for us tracings of all published figures, with the lateral views of skulls drawn facing the same way. Spreading these out side by side, sorting them into groups and making use of the published descriptions, and of our personal knowledge of the types, we grouped them into "clumps" and tried to draw up a workable definition of each.

Recently we have had the very great advantage of a publication by S. H. Haughton and A. S. Brink, "A bibliographical list of Reptilia from the Karroo Beds of Africa," *Palaeontologia Africana, II*, 1954. This is an admirable work, listing each species with a full set of bibliographic references, and giving the horizon and place of discovery of the type specimen. It provides also a series of families, and gives a diagnosis for each genus. The families we have set up were made independently, and chiefly before the publication of Haughton and Brink's list.

We were able to collaborate in this way because the senior author held an Alexander Agassiz Professorship in the Museum of Comparative Zoology in Harvard University in 1952, and was thus able to discuss the drawings Miss Townend (with help from the Royal Society) made for us. Thanks are due to these two bodies for their generosity.

In general we have carried the classification down to the genus only. In the case of the gorgonopsians, however, generic distinctions are none too certain in many cases and hence we have listed all species. We have not attempted subdivision of the dicynodonts, since much greater knowledge of skull structure than we possess today is needed before the systematics and evolution of this group can be unravelled. The vast majority of the therapsids listed are from South Africa; we have noted localities only for forms found in other regions. Stratigraphic horizons for types from South Africa and Russia are given in terms of the zones currently accepted for the Permian and Triassic of those regions.

ORDER THERAPSIDA

Advanced theropsid reptiles derived from the Pelycosauria. Characterised by the relatively great size and downturning of the paroccipital process so that it abuts directly against the inner surface of the squamosal opposite the inner side of the quadrate, not far above the articulation for the lower jaw. The temporal fossa is widened by an outpushing of the zygomatic arch, which is associated with a lateral extension of the squamosal. The posterior surface of this bone faces backward lateral to the ridge which bounds the area of attachment of neck muscles and lies at the outer end of the paroccipital process.

The quadrate is always attached to the quadratojugal in a characteristic theropsid manner, the latter bone resting upon the upper surface of the projecting outer condyle of the quadrate, being then separated from it by a quadratojugal foramen, and finally rising as a thin sheet closely applied to the posterior surface of the quadrate. It thus, to a greater or lesser extent, separates the quadrate from that depression on the front face of the lateral extension of the squamosal in which it lies. The suture between the epicondyle of the quadrate and the quadratojugal closes early, and has very rarely been seen. The quadrate-quadratojugal complex becomes much reduced, finally forming little more than a flattened nodule providing the articular surface for the lower jaw. In early forms the distal end of the stapes lies in a depression, the stapedial recess, in the inner edge of the quadrate, and in some later forms actually articulates directly with it, the stapedial recess vanishing.

The braincase is a massive structure, its component bones usually fusing early in life. The condyle always includes contributions from the exoccipitals, and in very advanced forms these alone remain functional, the basioccipital withdrawing from contact with the atlantal intercentrum. The proötic (which tends to be more expanded than in pelycosaurs), opisthotic and supraoccipital usually fuse early in life. The paroccipital process is massive and distally has a large abutment with the squamosal. Proximally the opisthotic joins with the proötic to form a fenestra ovalis completed by the posterolateral corner of the basisphenoid. The fenestra is placed very ventrally so that it is usually completely below the base of the brain. The floor of the

braincase, originally thick, becomes much thinner with time in the history of some groups, and may eventually be extremely reduced.

The basipterygoid process in the most primitive Russian form still articulates with the pterygoid by a smooth cartilage-covered surface. In all later forms the articulation is immobile and usually sutural. In general the process is converted into a flattened sheet of bone projecting horizontally and laterally well in front of the pituitary fossa. To it the pterygoid is attached below, and the epipterygoid rests on it. The anterior part of the brain usually lies in a sphenethmoid, a mesial bone resting on the upper border of a deep sheet of bone which is part of the basisphenoid extending forward below the pituitary fossa. Exceptionally the sphenethmoid resolves itself into a pair of orbitosphenoids.

Superficial membrane bones may, as in Dinocephalia, be roughened by an ornament, but in the later forms they are usually smooth (with such exceptions as the snout of *Cynognathus*). The membrane bones of the temporal region in early forms lie superficially, but later come to be closely attached to the braincase and largely buried by muscles. There is no supratemporal, and the dermosupraoccipital and tabulars, which long survive, lose all superficial exposure and become thin films "plastered" onto the posterior surface of the widened supraoccipital and parietals and the squamosals which border them. They never transgress the flange which marks the limits of attachment of the neck muscles on the squamosal. The parietals in early forms are widely expanded on the roof of the head, the brain cavity being limited by ridges on their ventral surfaces which may lie much mesial of the free border of the bone. They rest on the supraoccipital and are tied to it by the dermosupraoccipitals and tabulars. The lateral border of the parietal is primitively, and always to some extent, attached to a process from the postorbital which extends backward mesial to the temporal fossa, towards and in more primitive forms to the squamosal. In most forms the parietals separate to surround a pineal foramen, and in some groups are separated by a median preparietal bone. The parietals may form a deep and very narrow sagittal crest. The frontals are relatively small bones usually forming some part of the orbital margin. They are bordered by a postfrontal and, on

the final loss, by reduction in width, of that bone, by the postorbital which may itself be lost. Anteriorly they join the nasals and are bordered by the prefrontals. The lacrimal, short but always present, retains its superficial position.

The face may be very long, or very short, in specialised forms. It is seldom, if ever, pointed and usually is parallel sided, or even bulbous, so that the premaxillae are wide. In consequence the nostrils, in many groups, face as much forward as outward, and are often overhung by a projection of the nasal. There is a septomaxilla, with a superficial exposure in most early forms, withdrawn within the nasal cavity in some advanced animals. Sclerotic plates are occasionally present. There is some evidence which suggests that the latest therapsids possessed mammal-like turbinal bones in their very large muzzles, implying that they may have been warm blooded. The presence of large foramina on the face of late forms suggests that the skin was muscular and sensory and possibly had hairs, with the glands associated with them.

Primitively the quadrate ramus of the pterygoid, arising from the attachment to the basipterygoid process, passes directly to the quadrate, but in some advanced forms it may be cut short, scarcely extending behind the basipterygoid process, its place being taken by an epipterygoid process which may itself fail to reach the quadrate. The rest of the pterygoid stretches outward to make a transverse flange against the lower jaw, and forward to unite with the vomers and palatines to roof the mouth. The interpterygoid vacuity is reduced, often to a very small hole between the transverse flanges, or a narrow slit in advance of the basipterygoid processes. The palate so formed is greatly varied: it may be essentially flat, it may be largely vaulted, or it may bear a deep but narrow gulley passing backward from the posterior nostrils. In some forms, in differing ways, a secondary palate is formed so that the point at which inspired air enters the mouth becomes placed far back. In primitive forms the palate is continuous below the eye but in some a suborbital fenestra, between the pterygoid, ectopterygoid and palatine, makes its appearance. And this suborbital fenestra may in turn vanish with a re-expansion of the bones which surround it. A hyoid bone is not uncommonly seen; it stretches forward and inward from the neighborhood of the jaw articulation and pre-

sumably implies the presence of a muscular tongue.

The lower jaw is always compound, but the dentary may become very large and a place of muscle attachments. There is always a reflected lamina of the angular. There is usually a marginal dentition, and often palatal teeth, but all these may be lost and functionally replaced by horny sheets. The jaw articulation is opposite or anterior to the level of the occipital condyle. In some cases the lower jaw is capable of very free movements so as to grind up food in the mouth.

The vertebral column usually lacks intercentra, except anteriorly; the centra are usually not notochordal. To an increasing extent it is diversified, cervicals tend to be sharply distinguished from the dorsals which follow them, and a lumbar series with short fused ribs becomes established in later forms. There are usually at least three sacrals, and there may be as many as seven. The tail varies immensely in length, being sometimes as long as the rest of the body, sometimes a mere conical hinder end.

The limb girdles steadily become modernised, so that although a precoracoid and coracoid are always present the screw-shaped glenoid cavity of pelycosaurs is lost, and the precoracoid ceases to contribute to its surface at all. The clavicles are little expanded; short, broad interclavicles are universal. The cleithrum finally disappears. An ossified sternum is often present shewing the points of articulation of sternal ribs. The pelvis, at first pelycosaur-like, gains a thyroid fenestra; the iliac blade lengthens and approaches the mammalian position. The short pubis is still deflected anteriorly, and the ischium shortened.

Both fore and hind limbs become more advanced by bringing the elbow and knee in toward the body; thus the humerus becomes narrower and less twisted than in pelycosaurs and the femur gains an inturned head. The humerus always has an entepicondylar, and sometimes an ectepicondylar foramen. The deltopectoral crest is elongate. The number of digits is five in both hand and foot of all known therapsids. The numbers of phalanges, at first 2.3.4.5.4(3), is reduced to 2.3.3.3.3 in both fore and hind foot, an intermediate stage being known in which the primitive number of phalanges is retained but the third phalanx of the third toe, and the third and fourth of the fourth toe are reduced to very short discs. There is one centrale in the tarsus.

Distal carpal and tarsal five are absent. The effect of these changes is to raise the body of the animal off the ground, so that with the development of a digitigrade foot and the inturning of the elbow and knee, the animal's gait becomes very mammal-like, and its speed presumably largely increased.

There are apparently never any epiphyses in therapsids, so that residual cartilages of some substance seem to have remained (throughout life ?) in most members of the group.

The therapsids are customarily divided directly into a number of groups such as dinocephalians, dromasaurs, dicynodonts, theriodonts, etc. It appears, however, highly probable that at a very early stage in therapsid evolution there occurred a dichotomy resulting in two main lines, one including mainly carnivorous types and leading toward and to the mammals, the other consisting of herbivores, with the dicynodonts as its most conspicuous component. We therefore consider the order Therapsida as consisting of two suborders, here termed Theriodontia and Anomodontia. The former group is an expansion of the Theriodontia, as usually defined, to include, on the one hand, the carnivorous dinocephalians and, on the other, the ictidosaurs. In the Anomodontia are here included the herbivorous dinocephalians and dromasaurs as well as the dicynodonts. The present classification necessitates the division of the Dinocephalia as currently conceived. This last term is here restricted to the herbivorous forms (tapinocephaloids). The carnivorous forms (titanosuchids) fall into two groups, one of which may be called the Titanosuchia whilst the other includes certain very primitive members of the Gorgonopsia, the Phthinosuchidae.

SUBORDER THERIODONTIA

Therapsids generally with a carnivorous dentition in which there is a series of incisor teeth in the premaxilla, while the maxillary series contains towards its anterior end one or more enlarged teeth, the canines. The latter are usually oval in section and deep rooted. In some late forms this dentition may be converted (as in many mammals) into an herbivorous dentition by loss or reduction of the canine and modifications of the cheek teeth. Palatal teeth, usually restricted to thickened regions of the palatine and pterygoid, are commonly present in

members of the group. A tranverse flange, composed mainly of pterygoid but with a modest contribution from the ectopterygoid bone, always occurs; the quadrate ramus of the pterygoid arises abruptly from the flange, usually considerably dorsal to the admesial part of its lower border, and extends outwards toward and generally to the quadrate. This ramus, for a greater or less part of its length, touches the basisphenoid (in which the parasphenoid is included). At some point between the pterygoid flange and the posterior end of the basisphenoid (at the tubera which support the front part of the border — usually cartilaginous — of the fenestra ovalis) the pterygoid passes ventral to and is attached to the lower surface of a horizontal sheet of bone projecting outwards from the side of the basisphenoid. This projection is the basipterygoid process, whose upper surface is in contact with the base of the epipterygoid. The occipital aspect of the skull has a central area composed of the supraoccipital, the exoccipitals, and the usually powerful opisthotics, largely coated by the fused dermosupraoccipitals and tabulars. It is bounded by a backwardly projecting ridge, made jointly by the tabulars and squamosals with contributions from the parietals and interparietal in advanced forms. The supratemporal has completely vanished, and the posterior surface of the squamosal (lateral to the ridge) is usually of considerable width. The face is never greatly shortened; the lacrimal never reaches the septomaxilla.

In contrast to anomodonts, the face is not notably bent downward on occiput and suspensorium. The epipterygoid is usually broad. The suspensorium is never of great height, the jaw articulation being essentially in line with the tooth row and about at the level of the occipital condyle. The under surface of the skull tends to be flattened. The fenestra ovalis lies close to the ear cavity. A coronoid bone is present and a "coronoid process" frequently developed in the jaw.

Infraorder Titanosuchia

The parietal region broad, the temporal fossa lying largely on the outer side of the skull in early forms, its margin carried backwards on to a backwardly turned border of the squamosal. The face is long. There is no preparietal bone. Typically four

stout incisors, a prominent canine, usually circular in section, and a variable number — typically 8 to 16 — of small cheek teeth in both upper and lower jaws. The quadrate is a bone inserted in front of the lower border of the squamosal, but largely visible from behind. The external nostrils are narrow slits, floored largely by the septomaxilla, just touching the nasal, but largely surrounded by the premaxillae, whose internarial processes slope steeply backwards, separating the anterior ends of the nasals for a considerable distance. The lower jaw is shallow, with the articular surface directed largely backward and below the line of insertion of cheek teeth into the dentary. The reflected lamina is quite deep and its region of insertion lies far forward on the angular. Postfrontal present. No secondary palate. Paired vomers. No suborbital vacuities. Quadrate ramus of pterygoid well developed and of some height. Quadratojugal relatively large with laterally exposed area. Narrow ascending ramus of epipterygoid. Occipital condyle single. No projecting coronoid process. Cleithrum present. Little iliac expansion; no thyroid fenestra.

The titanosuchians have generally been included in the Dinocephalia, of which the typical members are large herbivores. Both are unquestionably primitive in many regards and in their most generalised members close to the base of the therapsid stock. But apart from primitive features the two groups have little in common except a clumsy build and a tendency toward thickening of the skull roof, both of which characters appear to be accompaniments of the usual large size.

Family Brithopodidae. Primitive titanosuchians, characterised by a face which is rather deep in proportion to its width and retains something of the triangular section found in *Dimetrodon*. The zygomatic arch is shallow and the temporal fossa large. The parietal foramen is very far back and the plane of the occiput nearly vertical. The quadrate is relatively short and not appreciably carried forward ventrally; the condyle is separated into two by an oblique spiral depression. Thickening and roughening of the bones of the skull is incipiently developed. Teeth are developed on the palate. The precoracoid enters the glenoid cavity, which retains a trace of its original screw shape. Phalangeal formula 2.3.3.3.3 in both limbs. The tail very long.

Very primitive therapsids from the Russian Permian. They were long known only from fragmentary remains, but Efremov has recently described a good skull of *Titanophoneus* and Orlov has given a general description of the skulls of *Admetophoneus* and *Syodon.*

Admetophoneus Efremov 1954, Russian zones I and II; *Brithopus* Kutorga 1838 (*Dinosaurus* Fischer 1847, *Eurosaurus* Fischer 1842, *Orthopus* Kutorga 1838, *?Rhopalodon* Fischer 1841), Russian zone I; *Syodon* Kutorga 1838 (*Cliorhizodon* Twelvetrees 1880), Russian zones I and II; *Titanophoneus* Efremov 1938, Russian zone II.

Limb bones found with brithopids are brigaded together as Phreatosuchidae by Efremov, and are remarkable because their structure includes many features which characterise pelycosaurs. They are described as *Phreatophasma* Efremov 1954, *Phreatosaurus* Efremov 1954, and *Phreatosuchus* Efremov 1954.

Family Anteosauridae. Titanosuchians of large size with skulls usually greatly thickened in aged individuals. The pineal foramen lies relatively far forward, but the intertemporal surface is wide, the postorbital strips being largely covered by muscle. The face is short, deep, and triangular in section (with a rounded median ridge). The frontal area is swollen and usually forms a brow over the snout. The facial processes of the premaxillae have a nearly straight dorsal border and extend far backward as narrow points between the nasals. Their dentigerous border slopes upward in front. The incisors are simple conical teeth which, with the canines, point somewhat forward; the numerous small maxillary teeth lie on a festooned border. The quadrate and attached quadratojugal are largely exposed below the squamosal, but continue the general direction of the hinder surface of that bone. The basis cranii is thin; the paroccipital process, though wide from back to front, is shallow.

Anteosaurus Watson 1921 (*Titanognathus* Broili and Schroeder 1935, *Dinosuchus* Broom 1936, *Broomosuchus* Camp, Taylor and Welles 1942), *Micranteosaurus* Boonstra 1954, *Paranteosaurus* Boonstra 1954, *Pseudanteosaurus* Boonstra 1954; all from the Tapinocephalus zone.

Family Jonkeriidae. Large titanosuchians with a very elongated face, wider than high and of nearly the same depth at the

nostril and the front of the orbit. The face is rounded in section and in no way triangular. The temporal region has a wide bar between the fenestrae, composed very largely of parietals, with the pineal foramen far forward. The temporal fossa is much smaller than in the Anteosauridae, and the quadrate very much larger, the quadratojugal attached to it being largely visible below the zygoma in a side view of the skull. The quadrate condyle faces largely forward and lies so far in front of the occiput that the temporal fossa appears floored by bone in direct dorsal view.

The palate lacks the tooth-covered thickenings found on the palate of the anteosaurs, and has enormously long and wide palatal nares, but is generally of similar type. The teeth carried by the widened premaxilla differ from those of *Anteosaurus* in that they possess basin-shaped crushing surfaces (like those of the tapinocephaloids) behind the high labial spike. The upper surface of the parietal and hinder part of the frontal are raised as a boss, a forehead standing out above the nearly straight mid-dorsal line of the face.

The jonkeriids as above described have a resemblance, which may be of importance, to the tapinocephaloids. Each group has an expanded cranial region from which a relatively small face projects forwards, and in each group certain members, at any rate, have the highly characteristic crushing premaxillary teeth best explained by Efremov in *Deuterosaurus*. These unique crushing incisors, taken with the development in each of a similar association of a swollen posterior part of the skull with a relatively slender face, suggest a community of origin, the two groups having parted from one another not very long before their first recognition at the base of the fossiliferous Karroo.

?*Archaeosuchus* Broom 1905 (not identifiable); *Dinartamus* Broom 1923; *Dinocynodon* Broom 1929; *Dinophoneus* Broom 1923; *Enobius* Broom 1923; *Glaridodon* Seeley 1888 (not identifiable); *Jonkeria* van Hoepen 1916 (*Dinosphageus* Broom 1929, *Dinopolus* Broom 1936); ?*Lamiasaurus* Watson 1914; *Phoneosuchus* Broom 1929; *Scapanodon* Broom 1904 (not identifiable); *Scullya* Broom 1929; *Titanosuchus* Owen 1879, all from the Tapinocephalus Zone.

Infraorder Gorgonopsia

Muzzle typically long and heavy. Temporal region relatively short, low and moderately expanded. Greatest skull width somewhat anterior to the quadrates. Dorsal processes of premaxillae relatively short here and in remaining theriodonts (in contrast to the titanosuchians).

The roof of the skull in the temporal region is wide, the postorbital meeting the squamosal and excluding the parietal from the border of the temporal fossa. There is in all later forms a preparietal bone, not usually in contact with the parietal foramen. The postfrontal is always present. The squamosal is attached medially to the parietal, tabular, and the end of the paroccipital process and laterally forms a thick transversely placed plate which turns forward to form the upper border of the zygomatic arch. Immediately lateral to the end of the paroccipital process the anterior face of the lower part of the squamosal is excavated into a recess, with a sharply defined upper border which may actually overhang the recess. Into this the quadrate and the adherent quadratojugal are received in such a way that much of the height of both bones is hidden by the squamosal in occipital view; in more advanced forms only a small proportion of the height of the quadrate can be so seen. There is no secondary palate, the choanae being very extensive openings which extend far back and in all later forms are enlarged on their outer sides anteriorly to form a hole through which the lower canine passes when the mouth is closed. In this and the following theriodont groups the vomers are fused. No suborbital vacuities. In Gorgonopsia, in contrast to the Therocephalia, the lateral border of the quadrate ramus of the pterygoid instead of following a straight line from its origin at the transverse flange, passes back parallel to the principal plane of the skull for a long way before turning out to join the quadrate, often with a curved border. This condition, though less well developed, anticipates the "girder" existing in higher cynodonts. The strap-shaped epipterygoid often has a quadrate ramus which may very nearly reach the quadrate. In the lower jaw the hinder end of the dentary projects freely above the surangular. Incisor teeth, usually 5 in number, are of large size; a precanine tooth in the maxilla very rarely occurs; there is a single canine and the

number of cheek teeth rarely exceeds 5. Palatal teeth occur. The digital formula is 2.3.4.5.4. The precoracoid is excluded from the glenoid cavity in this and the remaining theriodont groups. Little acromial development. Ilium little expanded; thyroid fenestra present.

The gorgonopsians are relatively primitive theriodonts, suggestive of ancestry to the cynodonts; however some features, such as the reduced cheek dentition indicate that typical gorgonopsians are aberrant to at least some extent. Most gorgonopsian skulls exhibit but minor variations on a fairly uniform pattern. For systematic purposes most might either be "lumped" in a single large family or divided into a considerable number of small families separated by relatively slight distinctions. The latter course is followed here, although in pursuing it there is found to be a number of genera in which proof is lacking of the distinctive qualities of any of the families erected.

Family Aelurosauridae. Gorgonopsians in which the intertemporal region is wide and the zygomatic arches probably do not spread widely. The snout is long but rather narrow in proportion to its depth, and the transverse section across it has a rounded upper margin. The dentition is 5.1.4-5, the dentigerous surface of the premaxilla sloping downward from the first incisor tooth, and the molar series inserted in a gently convex border of maxilla. The palate possesses teeth in irregular rows along the transverse flanges of the pterygoids, and there are sharply limited patches of teeth on the pterygoids and palatines posterior to the hinder ends of the internal nares.

This is a good recognizable group, but difficult to define.

"*Aelurognathus*" *serratidens* Haughton 1915, L. Cistecephalus zone; "*Aelurognathus*" cf. *serratidens* Broili and Schroeder 1934, Cistecephalus zone; "*Aelurognathus*" *sollasi* Broili and Schroeder 1935, U. Endothiodon zone; *Aelurosauroides watsoni* Boonstra 1934, Endothiodon zone; *Aelurosaurus felinus* Owen 1881 (*Aelurosaurus breviceps* Broom 1931, *Aelurosaurus striatidens* Broom 1912, *Aelurosaurus tenuirostris* Broom 1911, *Aelurosaurus whaitsi* Broom 1911), Endothiodon zone; "Gorgonopsier" Broili and Schroeder 1936, E. Africa, "Lower Bonebed."

Family Aelurosauropsidae. Small gorgonopsians characterised by the flattened face, which is nearly twice as wide as it is

high. The premaxilla below the nostril is deep, the face very little less than half the total length. The intertemporal width exceeds the interorbital. The pineal foramen touches the preparietal and is well behind the postorbital bar. The occipital condyle is the most posterior point of the skull.

Aelurosauropsis (*Aelurosauroides*) *wilmanae* Broom 1940, M.-U. Cistecephalus zone.

Family Arctognathidae. Advanced gorgonopsians with a short muzzle, rounded in section and with its tooth rows widely separated. The tooth-bearing lower border of the maxilla forms a large segment of a circle, the point of origin of the zygoma lying high up. Upper teeth 4.1.6. The intertemporal surface is narrow; the occipital surface meets it far forward; the preparietal lost or very small. The palate has a deep median trough extending back from the posterior nares, overhung by small tooth-bearing projections on the palatines. Behind the pterygoid flanges the pterygoid and parasphenoid form a narrow girder, the quadrate rami of the pterygoids taking off from it very far back and not reaching the quadrates. The lower surface of the basisphenoid forms a gently concave triangular area recalling that of cynodonts. The lower jaw is deep anteriorly, with a pronounced chin, and the dentary extends upward, free from the surangular, for a considerable distance.

Very recognizable forms.

Arctognathus curvimola Owen 1876, Cistecephalus zone; *Arctognathus whaitsi* Haughton 1924, M. Cistecephalus zone; *Lycaenodontoides bathyrhinus* Haughton 1929, Cistecephalus zone.

Family Arctognathoididae. Large gorgonopsians, characterised by a broad face which is about half the total skull length. The orbit is placed high up with a deep jugal below it. The temporal fossae are of moderate size and the occiput stretches forward between the fossae to their anterior ends. The pineal foramen, when present, lies just behind the parieto-frontal suture. There is usually no preparietal. Upper dentition 4-5.1.4-6. There are patches of teeth on the pterygoid and palatine.

"Aelurognathus" haughtoni Huene 1950, Lower Cistecephalus zone, E. Afr.; *Arctognathoides breviceps* Boonstra 1934, Cistecephalus zone; *Leontocephalus cadlei* Broom 1940, U. Cistecephalus

zone; *Leontosaurus vanderhorsti* Broom and George 1950, Cistecephalus zone.

Family Broomisauridae. Gorgonopsians with a relatively short, wide, and high face with a rounded upper surface. The continuous tooth-bearing border of the upper jaw is bowed downward, there being scarcely any trace of a step. The frontal enters the orbital margin by a narrow, parallel-sided process. The temporal fossa is short and wide, the temporal roof forming a third, or little more, of the extreme width. The occipital condyle lies far back.

Broomisaurus planiceps Broom 1913, Tapinocephalus or Cistecephalus zone; *Broomisaurus rubidgei* Broom 1940, Cistecephalus zone; *"Lycaenops" pricei* Broom and Robinson 1948, L. Cistecephalus zone.

?Family Burnetiidae (*Burnetiamorpha*). Small theriodonts in which the roof of the skull is thickened, shows in general no sutures, and is composed of fine cancellar bone, with essentially no superficial table of hard bone. There is a wide temporal roof, with laterally placed temporal fossae, presumably of gorgonopsian pattern. The palate lacks suborbital vacuities, has teeth on the pterygoids and palatines, and apparently a median groove; there may be 11 post-canine maxillary teeth.

The two animals reported to this family differ greatly in age. They may have been produced by parallel evolution from different parent stocks.

Burnetia mirabilis Broom 1923, U. Cistecephalus zone; *Styracocephalus platyrhynchus* Haughton 1929, U. Tapinocephalus zone.

Family Cynariopsidae. Gorgonopsians with a face which is never greatly elongated, rounded on its upper surface and with rather short temporal fossae. The most characteristic feature is the smooth curve made by the tooth-bearing margins of the premaxilla and maxilla which bring the anterior incisor so high up that the nose above it is extraordinarily shallow. Dentition 5.1.5 or thereabouts. There is a marked groove in the palate behind the posterior nares.

Cynarioides gracilis Broom, 1930, U. Endothiodon zone; *Cynarioides laticeps* Broom 1935, ?L. Cistecephalus zone; *Cyna-*

rioides tenuis Broom 1925, U. Endothiodon zone; *Cynariops robustus* Broom 1925, U. Endothiodon zone.

Family Galerhinidae. Small gorgonopsians with a rather flat skull in which the temporal fossa is markedly short, the occiput extends far forward, and the occipital condyle is the most posterior part of the whole skull. The family may be distinguished by the lack of a special, narrow, parallel-sided, orbital process of the frontal from some Tapinocephalus zone forms with otherwise comparable features. The zygomatic arch is noticeably shallow. The dentition is ?.1.5 in the upper jaw.

Galerhinus rubidgei Broom 1936, L.-M. Cistecephalus zone; *Galerhinus rubidgei* of Huene 1950. East Africa. ?Cistecephalus zone; *Galerhinus polyodon* Broom 1935, ?Cistecephalus zone.

Family Galesuchidae. Gorgonopsians in which the frontal enters the orbital margin as a more or less parallel-sided process between the prefrontal and very wide postfrontal. The temporal fossa is large and is not carried back as far as the level of the occipital condyle.

In *Galesuchus* the basicranial region forms a broad expansion ventral to the condyle, unknown in other gorgonopsian groups. In *Eoarctops,* which may belong here, there are 4 or 5 upper incisors, a canine and 3 molars arising from a continuous jaw margin which seems to show no sign of a step; in the lower jaw the coronoid process of the dentary projects above the surangular, the hinder part of the jaw being unusually deep.

Cerdodon tenuidens Broom 1915, Tapinocephalus zone; *Eoarctops vanderbyli* Haughton 1929, Tapinocephalus zone; *Galesuchus gracilis* Haughton 1915, Tapinocephalus zone; *Scylacognathus major* Broom 1935, L. Cistecephalus zone; *Scylacognathus parvus* Broom 1913, Tapinocephalus zone.

Family Gorgonognathidae. Large gorgonopsids, with a very long face exceptionally wide at the premaxilla-maxilla suture. The orbit is small (because of the animal's size), the temporal fossa rather small, with a very deep zygoma below it, the ventral border of the skull having a deep rounded notch below the orbit. The frontal reaches the orbit by a narrow process, as in *Dimetrodon.* Distinguished from Rubidgeidae by little except the entrance of the frontal into the orbit.

Gorgonognathus longifrons Haughton 1915, Cistecephalus

zone; *Gorgonognathus maximus* Huene 1950, E. Africa, L. Cistecephalus zone; *Gorgonorhinus luckhoffi* Broom 1937, ?L. Cistecephalus zone; *Gorgonorhinus minor* Broom 1948, ?L. Cistecephalus zone; *Tigricephalus kingwilli* Broom 1948, Cistecephalus zone.

Family Gorgonopsidae. Gorgonopsids in which the intertemporal region is comparatively wide and the zygomatic arches spread posteriorly. The snout is long and heavy, being both wide and high and the section across it a little in front of the eyes is noticeably square-cut. The squamosals are considerably laterally extended at the sides of the occiput and are shallow. The dentition is 5.1.1-5. A very marked step in the maxilla, raising the incisors above the canines and cheek teeth. A small sharply defined area of the pterygoid, near the midline, and on the level of the transverse flanges, bears small, sharp-pointed teeth. The basis cranii is very shallow, so that the condyle and paroccipital processes have very little height, and the posttemporal fossae lie very near the lower border of the occiput.

Gorgonops torvus Owen 1876, Endothiodon zone; *Leptotrachelus eupachygnathus* Watson 1912, Endothiodon zone; "*Lycaenops*" *kingoriensis* Huene 1950, E. Africa, L. Cistecephalus zone.

Family Hipposauridae. Gorgonopsians of small to middle size which are characterized by possessing a markedly curved dorsal contour; a very wide parietal region with much excavated occiput. The interorbital width is great and the orbits, always large, may become relatively enormous. The quadrate region is deep, produced forward as well as downward, and the quadrate itself projects very far below the ventral border of the squamosal and of the ridge made by the tabular. The articular border of the quadrate lies far below the basis cranii, the stapes passing as much downward as outward.

Hipposauroides rubidgei Broom 1940, Cistecephalus zone; *Hipposaurus boonstrai* Haughton 1929, U. Tapinocephalus zone; *Hipposaurus major* Boonstra 1952, Tapinocephalus zone; *Ictidorhinus martinsi* Broom 1913, U. Cistecephalus zone; *Lemurosaurus pricei* Broom 1949, L. Cistecephalus zone; *Pseudohipposaurus kitchingi* Broom 1948, ?Endothiodon zone.

Family Inostranceviidae. Gorgonopsians which reach a very large size. They have a very wide parietal region, with relatively

small temporal fossae. The occiput is very wide, stands nearly vertical, and the pineal foramen is immediately in front of its dorsal border. The paroccipital processes are deep. The face is long, its tooth-bearing border without a noticeable step. The dentary has a well marked "chin." The reflected lamina may bear a deep pocket on its lateral surface.

Distinguished from Rubidgeidae by lacking the extreme localised widening of the temporal region in later members of that family and the nearly circular widely separated temporal fossae.

Amalitzkia and *Inostrancevia* may be distinct genera.

Amalitzkia annae Pravoslavlev 1927, U. Permian, Russia; *Amalitzkia wladimiri* Pravoslavlev 1927, U. Permian, Russia; *Inostrancevia alexandri* Pravoslavlev 1927, U. Permian, Russia; *Inostrancevia latifrons* Pravoslavlev 1927, U. Permian, Russia; *Inostrancevia parva* Pravoslavlev 1927, U. Permian, Russia; *Inostrancevia proclivis* Pravoslavlev 1927, U. Permian, Russia.

Family Pachyrhinidae. Large gorgonopsids, in which the face is about as high as wide; the orbits small (no doubt owing to the overall size of the animal); the temporal fossae are relatively large, the bony roof which separates them being relatively narrow. The occipital condyle lies far in front of the posterior borders of the squamosals. The frontal reaches the orbit by a definite process between the pre- and large postfrontals. The dentition is 5.1.4 and there is no sign of a step. There is a small median groove behind the posterior nares.

Differs from Galesuchidae in the anterior position of occipital condyle. This may be largely a size effect. The frontal shape seems to be common in the Tapinocephalus zone.

Pachyrhinos kaiseri Broili and Schroeder 1934, U. Tapinocephalus zone.

Family Phthinosuchidae. The number of teeth is higher than in typical Gorgonopsia. The lower jaw shallow. The step in the dentition is little developed. The exposure of the squamosal lateral to the occipital surface is relatively very small. There is no preparietal? The pineal foramen is as posterior as possible.

Phthinosaurus Efremov 1938, Russian zone II (or III?); *Phthinosuchus* Efremov 1954, Russian zone I.

Family Rubidgeidae. A family of gorgonopsians, the mem-

bers of which attain very large size. The skull has a relatively large and narrow snout; the upper dentition being composed of a series of very powerful incisors, usually 5 in number, a canine, and a variable number of cheek teeth, ranging from 5 to 0. The maxilla has a rounded tooth-bearing border and is very deep. With increase in size, the whole temporal region increases in width ultimately to a very great extent, and this increase in general width goes with a corresponding and disproportionately enlarged broadening of the intertemporal region. The occipital region inclines forward and in large individuals reaches the pineal foramen, which lies immediately in front of the temporal openings. The occiput is necessarily very wide and the quadrates and squamosals do not seem to extend ventrally to the level of the occipital condyle. The palate lacks a suborbital vacuity and is of standard gorgonopsian pattern. A feature which may be rather characteristic is that the immensely deep anterior end of the mandible sweeps into the lower border of the jaw. The reflected lamina of the angular often bears a deep ridge, behind which are one, or two, deep pockets.

Dinogorgon (*Broomicephalus*) *laticeps* Brink and Kitching 1953, Cistecephalus zone; *Dinogorgon oudebergensis* Brink and Kitching 1953, Cistecephalus zone; *Dinogorgon quinquemolaris* Huene 1950, Cistecephalus zone, E. Africa; *Dinogorgon rubidgei* Broom 1936, M. Cistecephalus zone; *Dinogorgon* (*Dracocephalus*) *scheepersi* Brink and Kitching 1953, Cistecephalus zone; *Prorubidgea maccabei* (*pugnax*) Broom 1940, ?Cistecephalus zone; *Prorubidgea robusta* Brink and Kitching 1953, Cistecephalus zone; *Rubidgea atrox* Broom 1938, Cistecephalus zone; *Rubidgea kitchingi* Broom 1938, Cistecephalus zone; *Rubidgea laticeps* Broom 1940, U. Cistecephalus zone; *Rubidgea majora* Brink and Kitching 1953, Cistecephalus zone; *Rubidgea platyrhina* Brink and Kitching 1953, Cistecephalus zone; *?Smilesaurus ferox* Broom 1948, Endothiodon zone; *?Smilesaurus maccabei* Broom 1948, Endothiodon zone; *?Tangagorgon tenuirostris* Boonstra 1953, E. Africa, Lower Bone Bed; *Tigrisaurus pricei* Broom and George 1950, ?Cistecephalus zone.

Family Scylacocephalidae. Small gorgonopsians characterised by a long temporal fossa, the temporal roof being about twice as wide as the interorbital width. The snout is less than half the

total skull length, and is high and narrow. The frontal enters widely into the orbit. The lower jaw has a raised symphysial region, the canine socket being above the line of insertion of the cheek teeth. The hinder part of the jaw is unusually long and the reflected lamina deep and far forward.

Scylacocephalus watermeyeri Broom 1940, Cistecephalus zone.

Family Scylacopsidae. Small gorgonopsians in which the face forms about half the skull length. The face is rounded in cross section and widens gently, passing smoothly into the orbital region and so to the widest point of the skull about half way along the zygomatic arch.

The interorbital and intertemporal regions are of nearly equal width. The postorbital bones are of some width and pass down to rest on the zygoma by a widened arc. The temporal fossa is longer than is usual in gorgonopsids.

The occiput slopes forward; the squamosals are turned backward at their temporal border. There is a basioccipital with large tubera which join with those from the basisphenoid to support the cartilage surrounding the fenestra ovalis. The basisphenoidal tubera are separated by a pit but anteriorly are confluent and continued by a deep narrow ridge nearly to a very small interpterygoid vacuity.

Dental formula 4-5. 1. 4 (-7?).

Cyniscopoides broomi Brink and Kitching 1953, Cistecephalus zone; *?Cyniscops broomianus* Huene 1950, Cistecephalus zone, E. Afr.; *?Cyniscops cookei* Broom 1948, Cistecephalus zone; *?Cyniscops kitchingi* Broom 1948, Cistecephalus zone; *?Cyniscops longiceps* Broom 1941, Cistecephalus zone; *?Cyniscops rubidgei* Broom 1937, M. Cistecephalus zone; *Galerhynchus rubidgei* Broom 1937, Cistecephalus zone; "Gorgonopsid" Watson 1913, Cistecephalus zone; *Scylacops capensis* Broom 1913, Cistecephalus zone; *Sycocephalus bigendens* Brink and Kitching 1953, L. Cistecephalus zone.

Family Scymnognathidae. Gorgonopsids with a comparatively wide intertemporal region, and spreading zygomata. The snout is relatively long, square-cut in transverse section, and there is a marked step from the premaxilla to the maxillary tooth-bearing border. The paroccipital process is robust, deep below the posttemporal fossa, and the condyle and floor of the braincase thick.

Arctops willistoni Watson 1914, ?Endothiodon zone; *Chiwetasaurus dixeyi* Haughton 1926, Cistecephalus or U. Endothiodon zone, E. Africa; *Dixeya nasuta* Huene 1950, Cistecephalus zone, E. Africa; *Dixeya quadrata* Haughton 1926, Cistecephalus zone, E. Africa; *Lycaenoides angusticeps (minor)* Broom 1913, Cistecephalus zone; *Scymnognathus holmesi* Broom 1948, Endothiodon zone; *Scymnognathus major* Olson and Broom 1937, Endothiodon zone; *Scymnognathus parringtoni* Huene 1950, Endothiodon zone, E. Africa; *Scymnognathus whaitsi* Broom 1912, Endothiodon zone.

Family Sycosauridae. Gorgonopsians of medium size, with a face as long as the rest of the skull and rather heavily built, with a semicircular anterior end. Nostril very far above lower border of premaxilla. The postorbital bar is broad (cf. Rubidgeidae), the zygoma rather deep, the temporal fossa very short. The occiput is steeply inclined and makes a large bay with dorsal surface. The frontal is excluded from the orbital margin by a meeting of the pre- and postfrontals. There is no preparietal. Dentition 5. 1. 5.

Sycosaurus brodiei Broom 1941, Cistecephalus zone; *Sycosaurus laticeps* Haughton 1924, ?L. Cistecephalus zone.

Gorgonopsians represented by adequate skulls but lacking definite family characteristics:—Aelurognathus microdon Boonstra 1934, Cistecephalus zone; *Aelurognathus nyasaensis* Haughton 1926, Cistecephalus zone; *Aelurognathus tigriceps* Broom and Haughton 1913, Cistecephalus zone; *"Aelurognathus" minor* Brink and Kitching 1953, Cistecephalus zone; *Alopecorhynchus rubidgei* Brink and Kitching 1953, Cistecephalus zone; *"Arctops" watsoni* Brink and Kitching 1953, Cistecephalus zone; *Cerdorhinus parvidens* Broom 1936, U. Tapinocephalus zone; *Clelandina major* Broom 1948, Endothiodon zone; *Clelandina rubidgei* Broom 1948, U. Endothiodon or L. Cistecephalus zone; *Cyonosaurus longiceps* Olson 1937, L. Cistecephalus zone; *Lycaenops ornatus* Broom 1925, U. Endothiodon zone; *"Lycaenops" alticeps* Brink and Kitching 1953, Cistecephalus zone; *Nanogorgon gracilis* Broom and Robinson 1948, ?Cistecephalus zone; *Sauroctonus progressus* Hartmann-Weinberg 1938, Cistecephalus zone, Russia.

Gorgonopsians represented by material inadequate for proper assignment:—"Aelurosaurus" brevirostris Broom 1948, Endothiodon zone; *Aloposauroides tenuis* Brink and Kitching 1953, Cistecephalus zone; *Aloposaurus gracilis* Broom 1910, U. Endothiodon zone; *Arctosuchus tigrinus* Owen 1876, ?Endothiodon zone; *Cerdognathus greyi* Broom 1915, ?Cistecephalus zone; *Cynarioides grimbeeki* Broom 1935, U. Endothiodon zone; *Cyniscodon lydekkeri* Broom 1915, Tapinocephalus zone; *Cynodraco major* Owen 1876, L. Endothiodon zone; *Cynodraco serridens* Owen 1876, ?Endothiodon zone; *Delphaciognathus* (*Asthenognathus*) *paucidens* Broom 1915, Cistecephalus zone; *Eriphostoma microdon* Broom 1911, ?Tapinocephalus zone; *Genovum broilii* Huene 1950, Cistecephalus zone, E. Africa; *Lycaenodon longiceps* Broom 1925, L. Cistecephalus zone; *Lycosaurus pardalis* Owen 1876, ?Cistecephalus zone; *Pardocephalus wallacei* Broom 1948, Cistecephalus zone; "*Scymnognathus*" *parvus* Broom 1915, U. Endothiodon zone; *Tetraodon nowaki* Broili and Schroeder 1936, Endothiodon zone, E. Africa; *Tigrisuchus simus* Owen 1876, Cistecephalus zone; "unnamed gorgonopsian" Haughton 1924, M. Cistecephalus zone.

Infraorder Cynodontia

Advanced theriodonts, which possess a secondary palate but have no suborbital vacuities. There is a relatively narrow (or very narrow) sagittal crest formed almost entirely by the parietals, the postorbitals making only an infinitesimal addition to it. A parietal foramen is present. Postorbital bar always present. The temporal region is much expanded, with the greatest width posteriorly. The temporal opening faces more dorsally than laterally. The nasals are expanded posteriorly. The postorbitals do not meet the squamosals above the temporal fenestrae. The epipterygoid, widening dorsally, rises from the basipterygoid process to a long contact with the parietal. The posterior part of the basicranium has suffered so great a reduction of the basisphenoid tubera that they are no more than sharp-edged ridges bounding a triangular surface which extends more and more

posteriorly as time goes on. The occipital condyle is double or incipiently double. The posterior maxillary teeth have usually advanced beyond the stage of simple cones. The dentary is very large, posterior elements are much reduced, the reflected lamina of the angular usually reduced to a narrow process. There is no cleithrum; the anterior edge of the scapula is outturned, ending below in an acromial process. Coracoid elements are small. The ilium is greatly expanded. Generally a large obturator fenestra. Except in one primitive family the lumbar ribs are fused to the centra, and are shortened and interlocking. The phalangeal formula is always 2.3.4.5.3(4), but one intermediate phalanx in digit III and two such phalanges in digit IV are reduced to thin discs.

Cynodonts are present and not uncommon in the Cistecephalus, Lystrosaurus and Cynognathus zones of the Karroo series; these forms are here arranged in five families, those from the two lower zones being the more primitive. In addition, cynodonts are present in the late Permian of East Africa and northern Russia, and the Middle Triassic of South Ameriea and East Africa. A number of poorly known late Triassic therapsids may be late survivors of the group.

Family Procynosuchidae. Cynodonts in which the secondary plates of the maxillae and palatines do not always meet in the midline of the palate. The vagal foramen is relatively high up on the posterior surface of the skull. The occipital condyle is incipiently double in most forms. The quadrate margin lies very ventrally and the whole height of the quadratojugal is freely exposed in side and posterior views below and lateral to the posterior plate of the squamosal. In the lower jaw the hinder end of the dentary does not rise as a free process overhanging the surangular from their point of contact. Precanines present. Maxillary teeth normally all crenulated or tricuspidate and may be further elaborated.

Members of this primitive family are confined to the Cistecephalus zone of South Africa and presumably equivalent horizons in East Africa and Russia. "*Nanictosaurus*" *robustus* is probably a species of "*Nanictosuchus.*"

Drinia Amalitzky 1922, U. Permian, N. Russia; *Galcophrys* Broom 1948 (*Galecranium* Broom 1948), Cistecephalus zone; *Lea-*

vachia Broom 1948 (*Aleurodraco* Broom and Robinson 1948), Cistecephalus zone; "*Nanictosuchus*" Broom 1940, Cistecephalus zone; *Paracynosuchus* Broom 1940, Cistecephalus zone; *Parathrinaxodon* Parrington 1936, ?Cistecephalus zone, E. Africa; *Permocynodon* Sushkin 1929, U. Permian, N. Russia; *Procynosuchus* Broom 1937, Cistecephalus zone, E. Africa.

Family Thrinaxodontidae (*Galesauridae*). In this family and those which follow the secondary palate is complete and no precanine teeth are present. The vagal foramen is almost on the plane of the ventral surface of the basisphenoid. The occipital condyle is essentially double. The quadratojugal is not widely exposed from the side, its outer surface being covered by a ventral extension of the squamosal so that the bone is received in a special notch and is visible from behind. The dentary has a free coronoid process rising above the dorsal border of the surangular and directed backward. The posterior maxillary teeth are essentially conical, with minor cusps arising from the anterior and posterior borders of the central cone, these cusps not exceeding four in number. The teeth are in no way widened.

More advanced than the procynosuchids, this family is characteristic of the upper part of the Cistecephalus zone and the Lystrosaurus zone; *Sysphinctostoma* is a surviving Cynognathus zone form. Some material previously assigned to *Nythosaurus larvatus* and to *Galesaurus* pertains to *Thrinaxodon*.

?Baurocynodon Brink 1951, Cistecephalus zone; *Cynosaurus* Schmidt 1927, (*Cynosuchoides* Broom 1931, *Cynosuchus* Owen 1876), Cistecephalus zone; *Galesaurus* Owen 1859 (*Glochinodon* Hoepen 1916, *Glochinodontoides* Haughton 1924), Lystrosaurus zone; *Micrictodon* Broom 1937, Lystrosaurus zone; *Nanictosaurus* Broom 1936, U. Cistecephalus zone; *Notictosaurus* Broom 1936, base of Lystrosaurus zone; *Nythosaurus* Owen 1876, Lystrosaurus zone; *Platycraniellus* Hoepen 1917 (*Platycranion* Hoepen 1916), Lystrosaurus zone; *Sysphinctostoma* Broili and Schroeder 1936, Cynognathus zone; *Thrinaxodon* Seeley 1894 (*Ictidopsis* Broom 1912), Lystrosaurus zone.

Family Cynognathidae. Dentition carnivorous in type, the post-canine maxillary teeth apparently divided into "premolars" with simple crenulate crowns and "molars" with a series of cusps arranged nearly symmetrically about an enlarged central

member in a single anteroposterior row. The zygomatic arch is deep and broadly continuous posteriorly with the side of the braincase; its upper border not extending up to the level of the sagittal crest, and with a groove for the external auditory meatus some distance below its upper border. This family and the theriodont groups which follow (including the Ictidosauria) are distinguished from all other reptiles by the fact that the angle of the dentary is carried downwards as a free standing structure below the level of the ventral border of the hinder part of the jaw.

Of the common cynodonts of the Cynognathus zone with unexpanded "molars" most appear to belong to the genus *Cynognathus*, and supposed generic differences are mainly based on minor differences in the degree of development or stage of replacement of post-canine maxillary teeth; *Cynidiognathus* is distinguished by its short epipterygoid, which does not reach the quadrate. *Tribolodon* is, however, a very distinct form. *Karoomys* is perhaps the jaw of a young and indeterminate cynognathid. *Chiniquodon* and probably *Belesodon* of the Brazilian Middle Triassic appear to be late survivors of this family.

?Belesodon Huene 1936, M. Trias., S. Brazil; *Chiniquodon* Huene 1936, M. Trias., S. Brazil; *Cistecynodon* Brink and Kitching 1953, Cynognathus zone; *Cynidiognathus* Haughton 1922, Cynognathus zone; *Cynognathus* Seeley 1895 (*Cynogomphius* Broom 1932, *Lycaenognathus* Broom 1925, *Lycochampsa* Broom 1915, *Lycognathus* Broom 1913), Cynognathus zone; *Karoomys* Broom 1903, Cynognathus zone; "*Nythosaurus*" *browni* Broom 1912, Cynognathus zone; *Tribolodon* Seeley 1894, Cynognathus zone.

Family Diademodontidae. The post-canine maxillary dentition consists of a series of simple peglike "premolars," followed by a series of "molars" with transversely widened crowns, with a central ridge which in effect connects an outer and an inner cusp. The deep zygomatic arch is connected with the braincase through a shallow root. Its upper border lies on the level of the sagittal crest and descends abruptly behind, the whole being separated from the braincase, in posterior view, by a V-shaped notch. The external auditory meatus is deeply impressed; it is overhung by the outwardly rolled superior border of the zygoma.

The common genus of cynodont with expanded molars in the Cynognathus beds is that known alternatively as *Diademodon* or *Gomphognathus;* since the former has page priority, it is preferably used. *Cyclogomphodon* and *Octagomphus* are not generically separable from *Diademodon;* supposed generic and specific differences are largely based on dental differences which have to do with the state of wear or replacement of the 4 to 5 small "premolars," and variations, apparently in part ontogenetic, in the three posterior members of the molar series (which may run to a high count of ten). *Protacmon* is close to *Diademodon* but it differs in that the epipterygoid does not reach the quadrate. *Trirachodon* is a quite distinct type; *Trirachodontoides* is close to the last but distinct. *"Trirachodon" browni* is also distinct from that genus and merits a generic name. *Theropsodon and Traversodon* appear to be late surviving diademodontids.

Diademodon Seeley 1895 (*Cyclogomphodon* Broom 1919, *?Cynochampsa* Owen 1860, *Diastemodon* Seeley 1907, *Gomphognathus* Seeley 1895, *Microhelodon* Broom 1931, *Octagomphus* Broom 1919), Cynognathus zone; *Gomphodontoides* Brink and Kitching 1951, Cynognathus zone; *Inusitatodon* Brink and Kitching 1953, Cynognathus zone; *Protacmon* Watson 1920, Cynognathus zone; *Theropsodon* Huene 1950, M. Trias., E. Africa; *Traversodon* Huene 1936, M. Trias., S. Brazil, N. Argentina; *Trirachodon* Seeley 1895, Cynognathus zone; *"Trirachodon" browni* Broom 1915, Cynognathus zone; *Trirachodontoides* Broom 1932, Cynognathus zone.

Family Gomphodontosuchidae. This family is founded for the anterior part of a skull and lower jaw, which show a very short and extremely massive face, with relatively small incisors and canines and an entirely irregular series of post-canine teeth, about 6 in number, markedly angular in transverse section and with their grinding surfaces worn into a concavity.

Gomphodontosuchus Huene 1928, M. Trias., S. Brazil.

Cynodontia (?) incertae sedis.

The following are known from teeth, jaw fragments, jaws and other fragmentary remains from the Middle and Upper Triassic. While most, at least, appear to be late surviving cynodonts, it is not feasible to assign them systematically in the light of present knowledge.

Dromatherium Emmons 1857, U. Trias. NA.; *Exaeretodon* Cabrera 1943, M. Trias., N. Argentina; *Kunminia* Young 1947, U. Trias., E. Asia; *Lycorhinus* Haughton 1924, Redbeds, S. Africa; *Microconodon* Osborn 1886 (*Tytthoconus* Palmer 1903), U. Trias., NA.; *Pachygenelus* Watson 1913, Redbeds, S. Africa, (?Cynognathidae); *Theropsis* Cabrera 1943, M. Trias., N. Argentina, S. Brazil; *Tricuspes* E. Huene 1933, Rhaetic, Germany.

Infraorder Ictidosauria

Advanced therapsid reptiles with a secondary palate, no suborbital vacuities. The root of the zygomatic arch arises from the side of the maxilla well dorsally to and in advance of the last maxillary teeth. Tooth rows parallel or sub-parallel. No postorbital bar; no pre- or postfrontal or postorbital. The ascending ramus of the dentary arises far forward, lateral to and in front of the posterior cheek teeth. In contrast to cynodonts, the jaw articulation is far above the line of the teeth. The posterior elements of the lower jaw more reduced than in cynodonts.

This group was erected by Broom for the reception, primarily, of two small skulls, still unnamed, one with a partial skeleton, from the late Triassic Cave Sandstone of South Africa, which were obviously of a type advanced beyond the stage of any typical theriodont. With these specimens he later associated several other fragmentary remains, most of which, however, appear to be on a lower, cynodont level. Recent work indicates that the Tritylodontidae, long thought to be mammals, are advanced reptiles with a jaw construction of ictidosaurian type.

Family (unnamed). Short-snouted ictidosaurians, apparently without diastema. Maxillary teeth but little transversely widened, and incipiently bicuspidate transversely.

Including the "type" ictidosaurian material described but not named by Broom (1932); this material is at present being described by Mr. A. W. Crompton.

Family Tritheledontidae. Ictidosaurians with a long diastema and maxillary teeth placed very far posteriorly; cheek teeth numerous, transversely widened and bearing a single row of sharp-pointed cusps.

Tritheledon Broom 1912, Redbeds.

Family Tritylodontidae. Ictidosaurians with a narrow muzzle, on the lower surface of which is a very long diastema. One incisor both above and below, the lower procumbent. Cheek teeth quadrilateral in plan; the upper ones with three rows of wedge-shaped cusps, the lowers with two similar rows which bite into the grooves between the upper rows. Propalinal movement of the jaw results in longitudinal wear striae on the sides of the cusps and eventually in their complete flattening. The parasphenoid and basisphenoid form processes extending far below the level of the base of the braincase.

Our knowledge of these forms was long confined essentially to the fragmentary skull of *Tritylodon* from South Africa; recent discovery of a Chinese form described by Young and of numerous remains of *Oligokyphus* by Kühne indicates that we are dealing, not with multitubercular mammals as once thought, but with a somewhat parallel development from the ictidosaurian level of therapsid evolution. *Stereognathus* is the latest known theriodont.

Bienotherium Young 1940, U. Trias. Redbeds, E. Asia; *Chalepotherium* Simpson 1928, Rhaeto-Lias, Europe; *Oligokyphus* Hennig 1922 (*Mucrotherium* E. Huene 1933, *Uniserium* E. Huene 1933), Rhaeto-Lias, Württemburg and England; *Stereognathus* Charlesworth 1855, Stonesfield Slate, England; *Tritylodon* Owen 1884 (*?Triglyphus* Fraas 1866), Redbeds, South Africa, and ?Rhaeto-Lias, Württemburg.

?Family Microcleptidae (*Microlestidae*). Known only from molar teeth, which are oval, with a rounded basin bordered by cuspidate ridges.

These poorly known forms may be either advanced therapsids or archaic mammals, and are noted here merely for the sake of completeness (cf. Simpson).

Microcleptes Simpson 1928 (*?Hypsiprymnopsis* Dawkins 1864), Rhaeto-Lias, England; *Thomasia* Poche 1908 (*Microlestes* Plieninger 1847, *Plieningeria* Krausse 1919), Rhaeto-Lias, Württemburg and England.

Possible Mammals from the "Rhaetic." *Archaeodon* Huene 1925 (*Archaeotherium* Huene 1925), S. W. Africa; *Eozostrodon* Parrington 1941, England; *Morganucodon* Kühne 1949, England.

Infraorder Therocephalia

Theriodonts with a massively built skull in which the parietal forms a large part of the border of the temporal fossa, separating postorbital and squamosal by a large distance. Zygomatic and postorbital arches usually broad. There is no preparietal. The postfrontal usually present. The quadrate and quadratojugal are reduced and supported by the squamosal, as in gorgonopsids. The temporal region little expanded. Palatal plate long, basicranium short. Vomers paired; lower canines fit into pits in choanae. Usually a slit-like interpterygoid vacuity. The midventral line of the basisphenoid-parasphenoid complex behind the interpterygoid vacuity usually bears a very deep narrow midventral plate. There is no secondary palate but in some more advanced forms the central palatal strip is depressed so as to provide conditions which ultimately lead (cf. whaitsiids) to an arrangement which secures a comparable effect. The palate does not usually bear teeth. Suborbital vacuities usually present. The quadrate ramus of the pterygoid extends directly posterolaterally toward the quadrate, sending in a triangular flange to articulate with the basicranium. Occiput generally low and broad; condyle single. The jaw massive, the dentary deep. A coronoid process of the dentary present, rising well above the level of the surangular. Dentition strongly heterodont, with one or two large canines sharply set off from the adjacent teeth. Up to 7 incisors; usually no precanine maxillary teeth; up to 9 simple cheek teeth. A cleithrum primitively present. Little acromial development; scapular blade flat. Obturator fenestra little developed. No heel on calcaneum. The phalangeal formula is 2.3.3.3.3.

We include here a series of relatively primitive Permian theriodonts, generally of large size and massive build, the Pristerognathidae and Trochosuchidae, and their specialised descendants such as the Whaitsiidae and Euchambersiidae. More progressive forms, generally classed as therocephalians, are here brigaded with *Bauria* and its relatives in the Bauriamorpha.

Family Pristerognathidae. Large therocephalians with a narrow parietal crest, usually elevated; a parietal foramen situated well forward. A postfrontal, generally fairly large. The face is heavy and rounded in transverse section. The temporal fossae

are large, the quadrates unexpectedly small. The palate is essentially flat. There are large suborbital vacuities. The occiput is commonly deep, triangular in general plan and with a dermosupraoccipital which does not reach the summit of the back of the skull. The dentition usually includes a large number of incisors, up to 7; there is a single canine; the number of molars may reach 9 but may be as few as 3. There may be a small interpterygoid vacuity between the transverse flanges and sometimes another at the point where the deepened median parasphenoidal ridge separates the borders of the pterygoid. The lower border of the dentary is usually straight, rounding off to its anterior extremity. The two dentaries are usually not fused.

These are the characteristic therocephalians of the Tapinocephalus zone. *Pristerognathus*, *Scymnosaurus* and *Scylacosaurus* are known from good skulls, several others from skulls less complete; a number of genera are based on snout fragments, recognisable as belonging to this family but for the most part otherwise indeterminate.

Alopecideops Broom 1932; *Alopecodon* Broom 1908; *Alopecognathus* Broom 1915; *Alopecorhinus* Broom 1912; *Cynariognathus* Broom 1931; *Glanosuchus* Broom 1904; *?Hyorhynchus* Seeley 1889; *Ictidoparia* Broom 1925; *Ictidosaurus* Broom 1903; *Lycedops* Broom 1935; *Maraisaurus* Boonstra 1953; *Pardosuchus* Broom 1908; *Pristerognathoides* Boonstra 1954; *Pristerognathus* Seeley 1895; *Pristerosaurus* Boonstra 1954; *Ptomalestes* Boonstra 1954; *Scylacoides* Broom 1915; *Scylacorhinus* Broom 1915; *Scylacosaurus* Broom 1903; *Scymnosaurus* Broom 1903; *Therioides* Boonstra 1953; *Walteria* Brink and Kitching 1951; all from the Tapinocephalus zone.

Family Trochosuchidae. Large therocephalians which resemble the Pristerognathidae in fundamental features of their structure but differ in having a much lower skull, with a broad and rather flattened snout, a sagittal crest never elevated, and the occiput transversely widened. They may have 6 incisors and normally 2 canines, each separately replaced.

Hyaenasuchus Broom 1908; *Lycosuchus* Broom 1903; *Trochorhinus* Broom 1936; *Trochosuchus* Broom 1908 (*Trochosaurus* Haughton 1915); all from the Tapinocephalus zone.

Family Whaitsiidae. Therocephalians usually with a broad

shallow skull and a bulbous muzzle. The palate has a raised central area, roofed by the vomers and pterygoids. The sides of the deep groove are bordered by the palatines, which extend far forward, and the maxillae. In some forms special processes of the maxillae grow inwards from the admesial surface of these bones, in advance of the palatines, to meet the lateral margins of the vomers and thus divide the originally very long internal nostril into an anterior division for the reception of the lower canine and a functional nostril posteriorly; the anterior division may be reduced to a pit. The upper dentition contains 5 incisors and a large canine; there are normally no post-canine maxillary teeth, although in some forms (e.g., *Moschorhinus*) 2-5 small molars are to be seen, which are apparently early lost. As a result the lower border of the maxilla is much narrowed, the lateral surface of the face turning inward behind the canine to meet the palatal surface in such a manner as to suggest that the jaw was sheathed by a horny plate. In most forms a suborbital vacuity is absent; in some it is represented by a small opening, in others merely by a pit. The epipterygoid is widened. There is no interpterygoid vacuity. The lower border of the dentary forms a continuous, very well pronounced curve from the incisor border to its contact with the angular. The posterior part of the jaw is both large and deep; the reflected lamina of the angular is exceptionally well developed and sometimes fuses with the surangular so as to separate two foramina which pass down into the pocket which it occludes. The limbs are heavily built.

A Cistecephalus zone group, with molar reduction the most characteristic diagnostic feature. *Hofmeyria* of the Upper Endothiodon zone is apparently a forerunner.

Alopecopsis Broom 1920, Cistecephalus zone; *Hofmeyria* Broom 1935, U. Endothiodon zone; *Hycnosaurus* Broom 1935, M. or U. Cistecephalus zone; *Moschorhinus* Broom 1920, U. Cistecephalus and Lystrosaurus zones; *Moschorhynchus* Broom 1936, U. Cistecephalus zone; *Notaelurops* Broom 1936, L. or M. Cistecephalus zone, S. Africa, U. Perm., E. Africa; *Notosollasia* Broom 1925, U. Cistecephalus zone, S. Africa, U. Permian, E. Africa; *Promoschorhynchus* Brink 1954, Cistecephalus zone; *Theriognathus* Owen 1876, Cistecephalus zone; *Whaitsia* Haugh-

ton 1918 (*?Aneugomphius* Broom and Robinson 1948), U. Cistecephalus zone.

Family Euchambersiidae. A monotypic group, to include only *Euchambersia.* A therocephalian of medium size, with a face very broad for its length. The snout as far back as the canine has a rounded anterior border and a normal constitution, the septomaxilla being large and the septomaxillary foramen between it and the maxilla small. Behind the canine region the maxilla is very short and there is no indication of any articulation with a lacrimal or jugal; instead, its outer surface, over almost the whole of its height, is excavated into a great hemispherical cavity which communicates over a narrow notch with the palatal surface immediately behind the canine tooth. As this tooth, which otherwise is circular in section, bears a narrow ridge which arises abruptly from its outer surface, it is reasonable to regard this great chamber, which opens within the position of the lips, as housing a poison gland.

On the palate, the premaxillae, with indication of the presence of some 5 incisors on each side, have a narrow exposure continuing that of the anterior part of the maxillae. Nearly the whole of the posterior surface is in contact with the indented anterior ends of the vomers, which narrow as they pass backward to form the inner borders of the very elongate internal nares. These openings are widened and laterally produced anteriorly, presumably for the reception of the lower canines, but narrow posteriorly, where they are bordered on their outer sides by the palatines. The hinder border of the choana lies a considerable distance behind not only the canine but the point of entry of the poison gland duct. The vomers end posteriorly by expanding into a relatively large surface bordered by the palatine and pterygoid. The suborbital vacuities are reduced to foramina. There is the customary transverse flange, not carried far downward, but composed of a posterior pterygoidal and a somewhat larger transverse component. The flange passes forward to articulate powerfully with the posterior end of the maxilla immediately behind the notch for the poison gland. The condition is such as to make it most improbable that there was any zygomatic arch. The pterygoid extends backwards to a contact with the under surface of the basisphenoid. There are well-marked basisphenoidal tubera and a single occipital condyle. A widened

epipterygoid passes upward to the parietal.

The orbit is small and lacks any lower or posterior border. The only bone associated with it is the large prefrontal, which extends back to end by a contact with a reduced postorbital; the latter passes backward in contact with the frontal and parietal to form something of an inner wall of the temporal fossa. There is no parietal foramen. The frontal is exceptionally small; there is no lacrimal, postfrontal, jugal, squamosal or quadratojugal.

Euchambersia Broom 1931, Cistecephalus zone.

Therocephalia incertae sedis

The genera listed below are therocephalians which are not assignable to any of the families listed above, and do not show sufficiently distinctive features to merit the erection of further family groups for them. Most are from the Cistecephalus zone.

Anna Amalitzky 1922, U. Permian, N. Russia (cf. primitive whaitsiids); *Cerdops* Broom 1948, Cistecephalus zone; *?Cerdosuchoides* Broom 1936, ?Lystrosaurus zone; *?Cerdosuchus* Broom 1936, Cistecephalus zone; *Chthonosaurus* Vjuschkov 1955, U. Permian, Russia (cf. primitive whaitsiids); *Notaelurodon* Broom 1936, Cistecephalus zone; *Proalopecopsis* Brink and Kitching 1951, Cistecephalus zone; *?Theriodesmus* Seeley 1887, ?Cistecephalus zone.

Infraorder Bauriamorpha

Theriodonts descended from the Therocephalia and inheriting many of the features of that group, but characterized by the tendency to develop many advanced characters. The skull is usually lightly built, the face generally long and cylindroid; the temporal fossa generally relatively small. The zygomatic and postorbital arches are slender and the latter may be lost. No postfrontal. The parietal foramen is small or absent; the parietals frequently form a flat plate. Vascular foramina are usually present on the maxilla and may include a large forwardly directed opening leading to a depression on the premaxilla. A secondary palate is present or incipient in most cases. Suborbital vacuities large. An interpterygoid vacuity of large size whose anterior end lies between the transverse flanges is very commonly present. In many forms it extends backward onto the basisphenoid, separating the pterygoids quite widely and sometimes

ending abruptly at the level of a transverse suture visible on the ventral surface of the basisphenoid. To this point the perfectly straight, deep, quadrate ramus is attached by a slender flange of bone, usually with a concave ventral surface. The posterior border of this flange forms the end of a considerable space through which the projecting anterior part of the proötic may be visible. The basicranial tubera tend to spread widely and the proötic has a depression on its lateral surface whose admedian wall has an opening into the pituitary fossa, the roof lying horizontally and passing abruptly into the outer surface of the bone. The dentary is long but slender, with a continuously curved lower border which rises into a long ascending process, the prearticular forming a large internal flange below the articular. Dentition usually less heterodont than in therocephalians; the canines frequently reduced in prominence and less sharply marked off from the adjacent teeth; there may be several precanine maxillary teeth. The cheek teeth are usually small but cuspidate and may be numerous. The maxillary tooth row is markedly convex medially. Usually an ossified sternum and a very long, narrow, scapula blade. A small obturator fenestra. Calcaneum with heel; phalangeal formula 2.3.3.3.3.

We include here not only *Bauria* and other progressive Triassic forms with a secondary palate, but in addition a series of related families (scaloposaurids, etc.) which are usually included in the Therocephalia but appear to bear much the same relationship to the bauriids that the early cynodonts do to the typical Triassic members of that group.

Family Lycideopsidae. A monotypic family for *Lycideops.* A remarkable, large bauriamorph, with an elongated face and relatively small supratemporal fossa. The premaxillary teeth lie at a level considerably above that of the molars, there being a marked step in the dentition. Two upper canines are present and 10 small, uniform cheek teeth. In the lower jaw there are no incisors, but a canine and 5 minute, sparsely spaced cheek teeth.

Lycideops Broom 1931, U. Cistecephalus zone.

?Family Ictidosuchidae. A bauriamorph with a narrow face of considerable depth and a large and transversely wide temporal fossa. The parietal crest is high with a very sharp upper border.

There is an upper canine, and eight molars above and below, the anterior teeth being unknown.

Ictidosuchus Broom 1900, U. Endothiodon zone.

Family Nanictidopsidae. Bauriamorphs of medium size which lack a complete secondary palate. The head is not as broad or as depressed as in the Scaloposauridae. The interpterygoid vacuity is variable. The parietals form a crest; a parietal foramen is usually present. The postorbital arch is sometimes interrupted and is always slender. The basipterygoid is widened posteriorly. The dentition varies in count, but there are normally more than 4 and commonly 6 incisors; there are usually 2 precanine maxillary teeth, a distinct upper canine, and 6-10 cheek teeth (usually 9). All the teeth appear to be simple cones of circular section.

These Cistecephalus zone forms may represent the ancestors of *Bauria* and related types and, on the other hand, appear to be closely related to the Scaloposauridae.

Ictidosuchoides Broom 1931, Cistecephalus zone; *Ictidosuchops* Broom 1938, Cistecephalus zone; *Nanictidops* Broom 1940, Upper Cistecephalus zone; *Pelictosuchus* Broom 1940, ?Cistecephalus zone.

Family Silpholestidae. Small bauriamorphs with short temporal fossa and narrow but continuous postorbital bars. The parietal region, with a small parietal foramen, is broad and flattened. The zygomatic arch is slender and the articular surface of the quadrate not greatly depressed below it. The skull tapers to a narrow snout. The dentition retains many teeth — 6 incisors, 2-0 precanine maxillary teeth, a canine, and 10 or more cheek teeth. The angular is very deep and has an ornament of radiating ridges, a point of distinction from the somewhat similar scaloposaurids.

Ictidodraco Broom and Robinson 1948, ?L. Cistecephalus zone; *Scaloporhinus* Boonstra 1953, Cistecephalus zone; *Silphoictidoides* Huene 1950, L. Endothiodon zone, E. Africa; *Silpholestes* Broom 1948, U. Endothiodon zone; *Tetracynodon* Broom and Robinson 1948, Cistecephalus zone.

Family Scaloposauridae. Small bauriamorphs usually with an elongated face and a very short temporal region. Parietals normally form a broad flat area not perforated by a parietal foramen. Postorbital bar nearly always incomplete and postfrontal absent. The head as a whole low and very broad. No secondary

palate. The basisphenoid widens abruptly posteriorly and the proötic has a horizontal face directed downward, above the lateral opening to the pituitary fossa and mesial of the facial nerve foramen. The dentition always contains a large number of teeth which are little varied in that upper canines, though usually recognisable, are relatively small, and the incisors are not enlarged. There are typically 6 incisors; the canine is preceded by smaller maxillary teeth, numbering 2 or 3; there may be one or two enlarged canines; the postcanines are about 10 in number. The teeth are normally simple cones, but the cheek teeth may be incipiently tricuspidate. The lower jaw is exceedingly slender; the posterior end of the dentary rises little if any above the surangular.

Silphedocynodon and *Silphedestes* are not improbably scaloposaurids, in which both zygomatic and postorbital arches, always slender in this group, have been lost — either naturally, in the process of fossilization, or in preparation.

Choerosaurus Haughton 1929, M. Endothiodon zone; *?Homodontosaurus* Broom 1949, L. Cistecephalus zone; *Icticephalus* Broom 1915, Tapinocephalus zone; *Ictidodon* Broom 1925, Cistecephalus zone; *?Nanictocephalus* Broom 1940, Cistecephalus zone; *Scalopocephalus* Huene 1937, U. Endothiodon zone; *Scaloposaurus* Owen 1876, U. Cistecephalus or Lystrosaurus zone; *Scaloposuchus* Broom 1940, Cistecephalus zone; *Silphedestes* Broom 1949, M. Cistecephalus zone, ?Cynognathus zone; *Silphedocynodon* Brink 1951, M. Cistecephalus zone.

Family Ericiolacertidae. Very small bauriamorphs closely related to the Scaloposauridae but possessing a secondary palate. Suborbital vacuities and a relatively large interpterygoid vacuity present. The basisphenoid is expanded posteriorly. The skull is low. The postorbital bar is incomplete; there is no postfrontal. The parietals are wide. There is no parietal foramen. The dentition varies, but there is no well emphasized canine; the maxillary teeth may be elaborated.

?Cyrbasiodon Broom 1931, ?Lystrosaurus zone; *Ericiolacerta* Watson 1931, Lystrosaurus zone; Scaloposaurid indet. Broom 1932, ?Lystrosaurus zone.

Family Bauriidae. Advanced bauriamorphs with a secondary palate. There is a parietal crest, sometimes narrow; no pineal

foramen in most forms. The postorbital bar is slender and may be interrupted. There are well marked and separated basisphenoidal tubera, and the occipital condyle is notched as an incipient division. The lower incisors tend to be procumbent. The tooth rows diverge posteriorly, but are closer together than the width of the face above them, the surface of the maxilla flaring outward over a concavity to the lower border of the orbit and the face in front of it. The hinder part of the jaw is relatively large. The jaw articulation generally lies above the level of the cheek teeth. There are 4 large pointed incisors in the premaxillae, 1 canine, not noticeably larger than the incisors, and no precanine maxillary tooth. The cheek teeth (4 to 12) have crowns whose low irregular cusps were soon completely destroyed by wear. The crowns may be circular or transversely widened.

Aelurosuchus Broom 1906, Cynognathus zone; *Bauria* Broom 1909 (*Baurioides* Broom 1925), Cynognathus zone; *Melinodon* Broom 1905, Cynognathus zone; *Microgomphodon* Seeley 1895, Cynognathus zone; *Sesamodon* Broom 1905 (*Sesamodontoides* Broom 1950), Cynognathus zone; *Watsoniella* Broili and Schroeder 1935, Cynognathus zone.

Bauriamorpha incertae sedis

Akidnognathus Haughton 1918, Cistecephalus zone; *Blattoidealestes* Boonstra 1954, Tapinocephalus zone; *Haughtoniscus* Kuhn 1937 (*Macroscelesaurus* Haughton 1918), zone uncertain; *Ictidochampsa* Broom 1948, Cistecephalus zone; *Ictidognathus* Broom 1911, Cistecephalus zone; *Ictidostoma* Broom 1931, Endothiodon zone; *Nanictosuchus* Broom 1936, Cistecephalus zone; *Polycynodon* Broom and Robinson 1948 (*Octocynodon* Broom 1940), Cistecephalus zone; *Protocynodon* Broom 1949, Cistecephalus zone.

SUBORDER ANOMODONTIA

Therapsid reptiles usually of herbivorous habit. They are distinguished by the existence in them of a downwardly directed anterior part of the basioccipital whose morphologically ventral surface is directed backward below the condyle. The fenestra ovalis lies very ventrally, lateral to the downturned part of the basioccipital, and is connected to the rest of the labyrinth by a long downwardly directed tube filled with perilymph. Teeth are found only on the premaxilla, maxilla and dentary. Post-

orbital and squamosal meet above the temporal fenestra. Pterygoid flanges generally reduced and not sharply set off from the quadrate ramus. Deep suspensorium, extending far below tooth line and at a considerable angle to it. Quadrate and quadratojugal less reduced than in theriodonts. Ventral surface of skull not flattened as in many theriodonts. Jaw deep posteriorly, with a strongly curved dorsal margin descending posteriorly to the articulation. No coronoid process of dentary; no coronoid bone. Dentition usually highly modified or reduced. Phalangeal formula never exceeds 2.3.3.3.3.

Infraorder Dinocephalia

Primitive anomodonts in which the premaxillary teeth are often modified for crushing; the canine, at first large and of circular outline, is reduced to a point where it is no longer recognizable as a canine; the other maxillary teeth, at first simple cones, acquire, at least anteriorly, something of the crushing structure of the incisors. The postorbital part of the skull is short, the temporal fossa often wider than long, and the quadrate condyle carried far down below the base of the brain. The face is short, and often depressed and of feeble appearance, whilst the skull roof may be immensely thickened. Broad parietal table. Cheek deep, not greatly excavated in front of suspensorium. Squamosal not expanded laterally as in dicynodonts. Postfrontal always present. Premaxillae with long dorsal processes between nasals. No preparietal. Never any secondary palate, the choanae anteriorly placed. Body and limbs of massive build. Scapular blade flat; no acromion. Iliac blade little expanded, no obturator fenestra. Digits short, unguals broad.

As noted above we are restricting the term Dinocephalia to the tapinocephaloids.

Family Deuterosauridae. Primitive dinocephalians in which the skull is not pachyostotic to any great degree. The skull is very deep in proportion to its length, the relatively small orbit lying in the middle of its height, the face in front of it being of rather triangular section and largely made by a huge lacrimal. The temporal fossa is of great size, its ventral border lying on the same level as that of the orbit. It extends inwards so as

to be separated from its fellow only by a very narrow pair of parietals; these form a crest in front of the pineal foramen, which lies at the summit of the occiput. It is uncertain whether the squamosal and postorbital meet. The palate is triangular in plan with narrow premaxillae, which bear about 4 incisor teeth, each with a characteristic piercing cusp in front of a crushing heel. There is a large canine of nearly circular section and a few relatively simple maxillary teeth.

Deuterosaurus Eichwald 1846 (*Mnemeiosaurus* Nopcsa 1923, *Uraniscosaurus* Nopcsa 1928), Russia, zone I.

Family Moschopidae. Dinocephalia in which the skull is relatively high and narrow, the pachyostosis extending to many of the bones of the face and head, but being not very intense. There is no sharp distinction between the posterior part of the head and the face in the outline of the skull seen from the side. There is no enlarged canine, and the premaxillary and some maxillary teeth are of the type with a crushing heel, but some simple teeth are found in the maxilla behind the region where the canine should be, up to to the number of perhaps a dozen.

Delphinognathus Seeley 1892, probably Tapinocephalus zone; *Moschognathus* Broom 1914, U. Tapinocephalus zone; *Moschops* Broom 1911, Tapinocephalus zone; perhaps *Pnigalion* Watson 1914, Tapinocephalus zone.

Family Tapinocephalidae. Skull roof greatly thickened and rugose, often forming a brow above the apparently slender face which is always markedly separated from the postorbital region. The canine is never distinct, but the incisors vary from large teeth with a single cusp and a crushing heel to quite small structures (cf. *Mormosaurus*). There is a great variety of form expressed in a large number of generic names which may represent to some considerable extent different developmental stages. This family consists of most South African forms from the Tapinocephalus zone, and *Ulemosaurus* from zone II of Russia.

Agnosaurus Boonstra 1952, *Avenantia* Boonstra 1952, *Criocephalus* Broom 1928, *Eccasaurus* Broom 1909, *Keratocephalus* Huene 1931, *Mormosaurus* Watson 1914, *Moschoides* Byrne 1937, *Moschosaurus* Haughton 1915, *Pelosuchus* Broom 1905, *Phocosaurus* Seeley 1888, *Richeeckosaurus* Boonstra 1952, *Struthiocephaloides* Boonstra 1952, *Struthiocephalellus* Boonstra 1955,

Struthiocephalus Haughton 1915, *Struthionops* Boonstra 1952, *Tapinocephalus* Owen 1876, *Taurocephalus* Broom 1928, *Taurops* Broom 1912, *Ulemosaurus* Riabinin 1932.

Infraorder Venyukovioidea

Little or no pachyostosis. Lacrimal large and long. Suspensorium approaching dicynodont condition. Choanae placed in a deep pit, with the maxillae excluded from their borders. Teeth differentiated, with large anterior incisors, retention of a stout upper canine, and an irregularly placed series of small cheek teeth. Transitional in structure to the dicynodonts (cf. Watson 1948, Proc. Zool. Soc. London, vol. 118, pp. 823-77).

Family Venyukoviidae. This contains reptiles which are clearly intermediate between Dinocephalia and Dicynodontia. They are known from lower jaws and the anterior part of a skull. The dentition in the upper jaw is composed of three or four large grinding teeth in the premaxillae, the maxilla having a row of blunt teeth with rounded conical points. Posteriorly there is an incipient introduction of a second row of teeth. The posterior nares open into a deep depression on the palate surrounded by the palatines and premaxillae and divided into two by the vomers. The ectoptyerygoid bone is quite large and meets the pterygoid so as to form a low but characteristic flange against the inner surface of the lower jaw. Behind this the pterygoid soon ends; it is separated from its fellow by a small vacuity behind which it is attached to the basisceranium by a joint sutural surface. The rod-like quadrate ramus diverges from the basisceranium a short distance back of the transverse process. On the face, the maxilla is deep and appears to touch the prefrontal, excluding the lacrimal from the orbital border. The nostril lies some distance behind the end of the snout, and is underlain by a septomaxilla well exposed on the side of the face; the premaxillary processes separate the nasals almost to the level of the anterior part of the orbit. In the lower jaw the structure is essentially that of a dicynodont, but the dentary bears a row of teeth beginning with two enlarged procumbent teeth whose upper surfaces are worn by contact with the premaxillary teeth in the upper jaw. Farther back there is a pit on the widened upper surface of the dentary into which the

upper canine bites and behind this a series of pits for more posterior maxillary teeth. This part of the jaw must have been covered by horn, the dentary tooth row mesial to which is doubled. This genus provides a perfect intermediary stage in the development of dicynodonts from deuterosaurids.

?Rhopalodon Fischer 1841, Russia, zone I; *Venyukovia* Amalitzky 1922 (*Myctosuchus* Efremov 1937, *Venjukovia* Efremov 1940), Russia, zones I and II.

Infraorder Dromasauria

Small anomodonts with or without teeth, but with a lower jaw of dicynodont pattern. The squamosal wraps round the quadrate in a normal way and the zygoma arises on the most lateral part of the bone. The temporal fossa is short. The tail is long. There is no such development of the acromion as in dicynodonts. Coracoid elements large. Ilium little expanded; a small obturator fenestra. Feet slender, unguals claw-shaped.

The group Dromasauria was founded by Broom as a division of the Therapsida of equal value to the Dinocephalia, Anomodontia, etc. The entire group is represented by four individual animals belonging to three genera and species. The known specimens range in date from the middle of the Tapinocephalus zone to a horizon which appears to be in the middle of the Cistecephalus zone. The skull and lower jaw are known by unsatisfactorily preserved remains which do not allow of a complete description but do establish certain fundamental facts.

The only complete, uncrushed skull, the type of *Galepus jouberti*, has a very short muzzle with laterally directed nostrils; the orbit is very large, the frontals being bowed above it and passing backwards to the broad temporal region, which itself is directly continuous with a vertical occiput. The squamosals pass downward far below the level of the paroccipitals and occipital condyle so that the quadrate articular surface is carried down to a point well below the level of the teeth. The skull is preserved only as an internal mould in not very fine sandstone, and the condition of this mould makes it impossible to determine the position of the sutures between bones of the skull, though its general nature is obvious.

The lower jaw of this individual has a dentary whose upper border is slightly concave and bears a short row of some 6-7 teeth,

none larger than any other, not extending to the anterior end of the dentary and largely represented by casts of the alveoli in which they were placed. These alveoli are, in effect, impressed into the admedian surface of the dentary. The hind part of the jaw is of the same nature as that better seen in other specimens belonging to the group. Taken as a whole, the skull is characterized by the great size of the orbit, the short snout, and the very short temporal fossae.

Galechirus is represented by two specimens, one of which contains the impression of the outer surface of part of a skull and the lower jaw. The fragmentary skull resembles that of *Galeops* but shows evidence of the existence of teeth in both premaxilla and maxilla; there is no enlarged canine. In this specimen the lower jaw has no coronoid process on the dentary; the hinder part of the jaw resembles that of anomodonts in its possession of a fenestra between surangular, angular and dentary. The angular has a rounded lappet from its lower border which is no doubt a reflected lamina.

The single specimen of *Galeops* is contained in a split slab of very hard sandstone on which no preparation, apart from certain fractures, has been carried out. The skull is very high, apparently narrow, and short. The face is short, the external nostril very large, the orbit enormous and the temporal fossa deep, very narrow from back to front and separated from the orbit by a very narrow postorbital bar. The squamosal is continued far below the level of the base of the orbit, having a long free lateral border which extends downwards to the region of the condyle. Towards its dorsal end, where the squamosal comes up to the little broadened intertemporal roof, its posterior surface is rounded from side to side and produced a little backwards, as it is in many early therapsids. The suborbital bar, presumably largely composed of jugal, is exceedingly shallow. The quadrate is clearly visible but is not in a state to be described in any detail, though there is some reason for believing that it had a condyle divided by a median groove. It extends upwards, in contact with the front face of the descending process of the squamosal, to about the level of the lower border of the orbit.

The best preserved and most comprehensible part of the whole skeleton is the lower jaw. The dentary is a massive bone showing no signs whatever of teeth, unless a very curious notch, sur-

rounded by a peak in front and behind, which lies at the extreme front of the bone on its upper surface, is to be associated with a tooth insertion. The dentary extends backward to end in a small, backwardly projecting coronoid process, extending about a millimeter beyond the attachment to the surangular. The hinder part of the jaw includes an articular bone whose condylar face is directed backward and upward at an angle of about 45° with the length of the jaw and faces towards the condylar surface of the quadrate. As the bone is seen only in broken longitudinal section, the nature of the articular surface cannot be further described other than that it is convex as seen in side view, as in *Dicynodon*, is very extensive, and apparently ends immediately above a short, narrow, downturned process which is presumably an attachment for a posterior pterygoidal muscle, and not a retroarticular process. The surangular, which is continuous posteriorly with the articular, has a gently concave margin for the greater part of its length, and is overlapped on its outer surface by the upper border of the angular, the two bones separating to surround a foramen. The angular has a large reflected lamina passing downwards to a rounded lappet which extends several millimeters ventrally to the lower border of the body of the bone, when it extends backwards to overlap the articular at the root of the pterygoidal muscle process. In other words, the lower jaw is almost completely anomodont in structure.

The general nature of the postcranial skeleton is similar in all four dromasaur specimens. The essential features are that there is a distinct neck, with 5 to 7 cervical vertebrae; there is a back of some 20 vertebrae; the number of sacral vertebrae is not certainly known (? 2) and the tail is a relatively immense structure, with some 30-40 vertebrae, tapering very slowly, and probably as long as the presacral column and head together. Ribs in the cervical region are scarcely shown; they were presumably short. The dorsal ribs were long, fairly well curved and indicating the presence of a relatively slender body lacking, except perhaps in *Galeops*, the large size of the anomodont trunk. There is no definite evidence of specialized lumbar ribs. The caudal vertebrae seem to lack transverse processes, though they do carry chevron bones, at any rate in the proximal half of the tail. In three of the four specimens the tail is wrapped around the rest

of the body in such a way as to suggest a flexibility analogous to that of a squirrel or lemur, and is entirely unlike the lizard tail. The shoulder girdle has a large, rather wide, interclavicle, with an expanded and rounded hinder end; the scapula has a narrow, curved, blade expanding widely at the lower articular end, where it is attached to a rather small, perforate precoracoid and a larger coracoid. There is no sign of an ossified sternum or cleithrum. The humerus is a long, relatively narrow bone, with a slender shaft and not very expanded extremities, which lie only at a very small angle with one another in the later forms; there is an entepicondylar foramen. Radius and ulna are a little shorter than the humerus, subequal in size. There are 4 proximal and 5 distal carpals, with two centralia, one of which is exposed on the radial side of the carpus. The phalangeal formula is 2.3.3.3.3. The ilium is short, little expanded at the dorsal margin, and articulates directly with the pubis and ischium — rather flat, plate-like bones not separated by an obturator fenestra but with an unusually large pubic foramen. There is evidence that the ventral surface of the pelvis rose to a medial ridge. The femur is a slender bone, with no recognizable peculiarities; the fibula has a somewhat expanded upper end, extends slightly farther distally than the tibia and leaves a rather wide interosseous space between the two bones. The astragalus is a bone of considerable size which articulates with a face on the admedian border of the calcaneum, there being some evidence of a notch between the two. The calcaneum is a large bone, extending laterally to its contact with the fibula and the fifth metatarsal. There are four distal tarsals, the fourth being much the largest; a single centrale separates the astragalus from the first to third distal tarsals. The phalangeal formula is 2.3.3.3.3. There is evidence of the existence of some abdominal ribs a little in front of the pelvis.

Broom, in his early discussions, held that the Dromasauria was a group of equivalent rank to the Dinocephalia or the dicynodonts, but in the "Mammal-like Reptiles of South Africa" (1932) which appears to be his last statement on the matter, he withdrew a little from this view, stating that it is impossible to say whether the dromasaurians are a primitive group or dwarf aberrant descendants of early therocephalian ancestors.

To anyone who is familiar with dicynodont structure, or even

with the structure of *Venyukovia*, there is evident a remarkable, rather detailed dicynodont appearance in the lower jaw of *Galeops*. This is, in effect, so striking that we do not think anyone presented with the lower jaw of this animal would come to any conclusion other than that it was a dicynodont of slightly unusual character. This resemblance depends in part on the lack of teeth in the dentary, largely on the remarkably massive dentary as a contrast to the rather less massive hinder part of the jaw; even the texture of the bone of the dentary, as seen in fracture, is extraordinarily like that of a dicynodont. The surangular and angular are precisely those of a small dicynodont, even to the rather characteristic shape of the reflected lamina. The general nature of the articular, so far as it can be seen in the longitudinally fractured specimen is, again, dicynodont-like, and the dorso-ventrally convex hinder part of its articular surface is a character known in no therapsid group except the anomodonts.

The way in which the alveoli of the cheek teeth of the *Galepus* jaw are as it were, notched into the inner surface of the dentary can be matched only in endothiodonts, where the condition has arisen as a result of the development of a dicynodont horny beak lateral to the teeth. The long ventral process of the squamosal, which supports the quadrate, is another dicynodont quality, but the external view of the battered hinder part of the squamosal which is seen on the back of the counterpart of the slab of *Galeops* seems to show no trace or, at any rate, no more than a beginning of that lateral production of the descending part of the squamosal which is characteristic of dicynodonts. The extraordinarily short temporal fossa of all dromasaurians is a point of extreme contrast to the dicynodonts, in which the temporal fossa is (except secondarily, in such forms as *Lystrosaurus*) of quite exceptional length.

The dicynodonts as a whole are animals with a head of normal size which is connected by a neck which would appear short to an extraordinarily broad and deep trunk. Even in small forms comparable in size to the Dromasauria the tail is short and conical, the limbs short and heavily built; further, all the bones from humerus to phalanges are thick in proportion to their length and the claws in which both fingers and toes end, appear never to be laterally compressed and slender but are usually

markedly broad and flat. There is indeed no resemblance between the posteranial skeletons of individuals of the two groups other than that implied by the statement that they are therapsids.

Galechirus Broom 1907, zone uncertain; *Galeops* Broom 1912, U. Tapinocephalus zone; *Galepus* Broom 1910, zone uncertain.

Infraorder Dicynodontia

Anomodonts in which the dentition, no doubt complete and marginal in their ancestors, tends to disappear as it is supplemented and ultimately replaced by a horny beak, analogous to that of a tortoise, in both upper and lower jaws. The animals were certainly herbivorous, and the skull becomes a unique structure designed to house a very powerful musculature which enables the heavy lower jaw to crush food against the palate, and, in all probability, to bite a large mass from such a thing as a cycadean trunk. In the great majority of known forms very powerful canine tusks are found in the males, such structures being completely lacking in females, and therefore forming no part of the feeding mechanism. The dentaries are always fused at a short and very heavy symphysis whose lower surface stands largely vertical. The squamosal has a unique structure in that its body forms a flat sheet continuing the occipital surface. From the front face of the squamosal the zygoma projects abruptly so that its upper border meets that of the body of the squamosal at a point, whilst its lower border passes into the middle of the body. There thus arises a special large space for a masseteric muscle cut off from the larger temporal mass by the flat sheet of the posterior part of the zygoma. The temporal fossa is long.

In the more primitive dicynodonts a wide roof of parietals bordered by postorbitals and squamosals separates the very large temporal fossae, the pineal foramen which perforates it often impinging on a preparietal bone. The face is short (in the more advanced forms very short) in comparison with the huge temporal region. The face is bounded anteriorly by the premaxillae which descend to form a ridge round the anterior end of the palate. They are always fused with one another and their internarial process, which rises at first directly upwards and then passes round a segment of a circle towards the upper surface of the skull, separates the deeply impressed nostrils by a considerable space, and reaches the nasals. The maxillae, from their

suture with the premaxillae, rise to meet the nasals and form part of the border of the nostril, though the septomaxilla, which is usually well developed, has often a considerable facial exposure, and may exclude them from that opening. The maxilla never has any marginal teeth except for the very large canines of the males, whose long root extends upwards within the borders of the bone so as to gain support for the projecting tusk. The tooth is circular in section. The point on the maxilla where the tooth arises is often projected down as a very long process which also occurs in females in which the tusk is missing. In the more primitive forms, "endothiodonts," teeth occur on the palate mesial of the canine (if present). They are actively replaced and usually have ridged pointed crowns, often with a saw edge on one side. They occur usually in the maxilla, and occasionally also in the premaxilla. It is evident that this tooth row is not palatal, but is the original therapsid series. A similar development of teeth in the lower jaw is usually inserted in the lingual side of the dentary. The body is ordinarily very bulky, but with a definite neck. The fore and hind feet have a digital formula of 2.3.3.3.3. The limbs are short and strong and the claws flattened and obviously powerful. The stride is short compared with the width of track. There is on the scapula a definite acromial process, within which lay a prespinous muscle. The precoracoid is excluded from the glenoid cavity and there is a sternum. The pelvis has an ilium widened dorsally and a sacrum of from 3 to 7 vertebrae. There is an obturator foramen and the ventral borders of the pubis and ischium do not always meet their fellows in symphysis.

We have made no attempt at an arrangement of the genera of dicynodonts, of which more than fourscore have been described.

THERAPSIDA INCERTAE SEDIS

Arnognathus Broom 1907, ?Cistecephalus zone; *Dimacrodon* Olson and Beerbower 1953, L. or M. Permian of North America; *Herpetochirus* Seeley 1895, ?Lystrosaurus zone; *Mygalesaurus* Broom 1942, Cistecephalus zone; *Mygalesuchus* Broom 1942, Cistecephalus zone; *Rubidgina* Broom 1942, Cistecephalus zone; *Simorhinella* Broom 1915, Tapinocephalus zone; *Tamboeria* Seeley 1904, Tapinocephalus zone; *Theromus* Seeley 1895, ?Lystrosaurus zone.

Admetophoneus, 49
Aelurodraco, 63
Aelurognathus, 52, 53
Aelurosauroides, 52, 53
Aelurosauropsis, 53
Aelurosaurus, 52, 61
Aelurosuchus, 76
Agnosaurus, 78
Akidnognathus, 76
Alopecideops, 69
Alopecodon, 69
Alopecognathus, 69
Alopecopsis, 70
Alopecorhinus, 69
Alopecorhynchus, 60
Aloposauroides, 61
Aloposaurus, 61
Amalitzkia, 57
Aneugomphius, 71
Anna, 72
Anteosaurus, 49
Archaeodon, 67
Archaeosuchus, 50
Archaeotherium, 67
Arctognathoides, 53
Arctognathus, 53
Arctops, 60
Arctosuchus, 61
Arnognathus, 86
Asthenognathus, 61
Avenantia, 78
Bauria, 76
Baurioides, 76
Baurocynodon, 63
Belesodon, 63
Bienotherium, 67
Blattoidealestes, 76
Brithopus, 49
Broomicephalus, 58
Broomisaurus, 54
Broomosuchus, 49
Burnetia, 54
Cerdodon, 55
Cerdognathus, 61
Cerdops, 72
Cerdorhinus, 60
Cerdosuchoides, 72
Cerdosuchus, 72
Chalepotherium, 67
Chiniquodon, 63
Chiwetasaurus, 60
Choerosaurus, 75
Chthonosaurus, 72
Cistecynodon, 64
Clelandina, 60
Cliorhizodon, 49
Criocephalus, 78
Cyclogomphodon, 65
Cynariognathus, 69
Cynarioides, 54, 61
Cynariops, 55
Cynidiognathus, 64
Cyniscodon, 61
Cyniscopoides, 59
Cyniscops, 59
Cynochampsa, 65
Cynodraco, 61
Cynognathus, 64
Cynogomphius, 64
Cynosaurus, 63
Cynosuchoides, 63
Cynosuchus, 63
Cyonosaurus, 60
Cyrbasiodon, 75
Delphaciognathus, 61
Delphinognathus, 78
Deuterosaurus, 78
Diademodon, 65
Diastemodon, 65
Dimacrodon, 86
Dinartamus, 50
Dinocynodon, 50
Dinogorgon, 58
Dinophoneus, 50
Dinopolus, 50
Dinosaurus, 49
Dinosphageus, 50
Dinosuchus, 49
Dixeya, 60
Dracocephalus, 58
Dromatherium, 66
Dvinia, 62
Eccasaurus, 78
Enobius, 50
Eoarctops, 55
Eozostrodon, 67
Ericiolacerta, 75
Eriphostoma, 61
Euchambersia, 72
Eurosaurus, 49
Exaeretodon, 66
Galechirus, 85
Galecranium, 62
Galeophrys, 62
Galeops, 85
Galepus, 85

Galerhinus, 55
Galerhynchus, 59
Galesaurus, 63
Galesuchus, 55
Genovum, 61
Glanosuchus, 69
Glaridodon, 50
Glochinodon, 63
Glochinodontoides, 63
Gomphodontoides, 65
Gomphodontosuchus, 65
Gomphognathus, 65
Gorgonognathus, 55
Gorgonops, 56
Gorgonorhinus, 56
Haughtoniscus, 76
Herpetochirus, 86
Hipposauroides, 56
Hipposaurus, 56
Hofmeyria, 70
Homodontosaurus, 75
Hyaenasuchus, 69
Hycnosaurus, 70
Hyorhynchus, 69
Hypsiprymnopsis, 67
Icticephalus, 75
Ictidochampsa, 76
Ictidodon, 75
Ictidodraco, 74
Ictidognathus, 76
Ictidoparia, 69
Ictidopsis, 63
Ictidorhinus, 56
Ictidosaurus, 69
Ictidostoma, 76
Ictidosuchoides, 74
Ictidosuchops, 74
Ictidosuchus, 74
Inostrancevia, 57
Inusitatodon, 65
Jonkeria, 50
Karoomys, 64
Keratocephalus, 78
Kunminia, 66
Lamiasaurus, 50
Leavachia, 62-63
Lemurosaurus, 56
Leontocephalus, 53
Leontosaurus, 54
Leptotrachelus, 56
Lycaenodon, 61
Lycaenodontoides, 53
Lycaenognathus, 64
Lycaenoides, 60
Lycaenops, 54, 56, 60
Lycedops, 69
Lycideops, 73
Lycochampsa, 64
Lycognathus, 64
Lycorhinus, 66
Lycosaurus, 61
Lycosuchus, 69
Macroscelesaurus, 76
Maraisaurus, 69
Melinodon, 76
Micranteosaurus, 49
Micrictodon, 63
Microcleptes, 67
Microconodon, 66
Microgomphodon, 76
Microhelodon, 65
Microlestes, 67
Mnemeiosaurus, 78
Morganucodon, 67
Mormosaurus, 78
Moschognathus, 78
Moschoides, 78
Moschops, 78
Moschorhinus, 70
Moschorhynchus, 70
Moschosaurus, 78
Mucrotherium, 67
Myctosuchus, 80
Mygalesaurus, 86
Mygalesuchus, 87
Nanictidops, 74
Nanictocephalus, 75
Nanictosaurus, 63
Nanictosuchus, 63, 76
Nanogorgon, 60
Notaelurodon, 72
Notaelurops, 70
Notictosaurus, 63
Notosollasia, 70
Nythosaurus, 63, 64
Octagomphus, 65
Octocynodon, 76
Oligokyphus, 67
Orthopus, 49
Pachygenelus, 66
Pachyrhinos, 57
Paracynosuchus, 63
Paranteosaurus, 49
Parathrinaxodon, 63
Pardocephalus, 61
Pardosuchus, 69

Pelictosuchus, 74
Pelosuchus, 78
Permocynodon, 63
Phocosaurus, 78
Phoneosuchus, 50
Phreatophasma, 49
Phreatosaurus, 49
Phreatosuchus, 49
Phthinosaurus, 57
Phthinosuchus, 57
Platycraniellus, 63
Platycranion, 63
Plieningeria, 67
Pnigalion, 78
Polycynodon, 76
Pristerognathoides, 69
Pristerognathus, 69
Pristerosaurus, 69
Proalopecopsis, 72
Procynosuchus, 63
Promoschorhynchus, 70
Prorubidgea, 58
Protacmon, 65
Protocynodon, 76
Pseudanteosaurus, 49
Pseudohipposaurus, 56
Ptomalestes, 69
Rhopalodon, 49, 80
Riebeeckosaurus, 78
Rubidgea, 58
Rubidgina, 87
Sauroctonus, 61
Scalopocephalus, 75
Scaloporhinus, 74
Scaloposaurus, 75
Scaloposuchus, 75
Scapanodon, 50
Scullya, 50
Scylacocephalus, 59
Scylacognathus, 55
Scylacoides, 69
Scylacops, 59
Scylacorhinus, 69
Scylacosaurus, 69
Scymnognathus, 60, 61
Scymnosaurus, 69
Sesamodon, 76
Sesamodontoides, 76
Silphedestes, 75
Silphedocynodon, 75
Silphoictidoides, 74
Silpholestes, 74
Simorhinella, 87
Smilesaurus, 58
Stercognathus, 67
Struthiocephalellus, 78
Struthiocephaloides, 78
Struthiocephalus, 79
Struthionops, 79
Styracocephalus, 54
Sycocephalus, 59
Sycosaurus, 60
Syodon, 49
Sysphinctostoma, 63
Tamboeria, 87
Tangagorgon, 58
Tapinocephalus, 79
Taurocephalus, 79
Taurops, 79
Tetracynodon, 74
Tetraodon, 61
Theriodesmus, 72
Theriognathus, 70
Therioides, 69
Theromus, 87
Theropsis, 66
Theropsodon, 65
Thomasia, 67
Thrinaxodon, 63
Tigricephalus, 56
Tigrisaurus, 58
Tigrisuchus, 61
Titanognathus, 49
Titanophoneus, 49
Titanosuchus, 50
Traversodon, 65
Tribolodon, 64
Tricuspes, 66
Triglyphus, 67
Trirachodon, 65
Trirachodontoides, 65
Tritheledon, 67
Tritylodon, 67
Trochorhinus, 69
Trochosaurus, 69
Trochosuchus, 69
Tytthoconus, 66
Ulemosaurus, 79
Uniserium, 67
Uraniscosaurus, 78
Venjukovia, 80
Venyukovia, 80
Walteria, 69
Watsoniella, 76
Whaitsia, 70

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By George B. Wislocki
and
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Department of Anatomy, Harvard Medical School,
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With Eight Plates

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No. 3 — The Placenta of the Wolverine (*Gulo gulo luscus* (Linnaeus))[1]

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INTRODUCTION

Of the numerous fissiped carnivores the placentation of perhaps fifteen species has been to some degree studied. It is of interest when a specimen becomes available of a genus or species in which the placenta has not been described before, and thus we were fortunate in obtaining the placenta of a wolverine. This animal is a member of the family of Mustelidae of the genus *Gulo*, of which, according to Weber ('28), there are two species, the Eurasian glutton, *G. gulo* L. and the North American wolverine, *G. luscus* L.; others, however, regard the animals of the two continents as conspecific (cf. Rausch '53). The placenta of neither of these species has been described before.

The placentation of various other members of the Mustelidae is to some extent known. Nearly a century ago Bischoff (1865 a, b), reported on the placentation of martins (*Mustela foina*, *Mustela martes*), the weasel (*Mustela vulgaris*), and the otter (*Lutra vulgaris*), while more recently the placenta of the ferret (*Putorius furo*) has been described by Robinson ('04) and Strahl and Ballmann ('15), and that of *Zorilla* by Rau ('25).

MATERIAL AND METHODS

The present specimen consists of a pregnant uterus (with the ovaries removed) of a wolverine (*Gulo gulo luscus* (Linnaeus)) collected on February 9, 1954, at Mt. Susitna, near Anchorage, Alaska. The specimen was presented to us for study through the interest and courtesy of Dr. Robert Rausch, Chief, Animal-borne Disease Branch, Arctic Health Research Center, Anchorage, Alaska, whose taxonomic terminology we have accepted. The uterus with one of the gestation sacs laid open to ensure better fixation was preserved in a 10% solution of formaldehyde.

The specimen was first studied grossly by inspection and dissection. Then representative pieces of the placentas, fetal mem-

[1] Aided by a grant (G-2298(C3)) from the U. S. Public Health Service, National Institutes of Health, and the Eugene Higgins Trust of Harvard University.

branes and umbilical cords were removed. These were imbedded in paraffin, sectioned and stained. The sections were stained by means of Masson's trichrome stain, Gomori's ('41) chrome alum-hematoxylin and phloxine stain and McManus' periodic acid-Schiff stain. The stained sections were cleared and mounted in clarite. We are indebted to Miss Etta Piotti for three excellent drawings of parts of the specimen.

GROSS ANATOMY

The specimen consists of a bicornuate uterus containing one gestation sac in the right cornu and two gestation sacs in the left horn. The three sacs are practically identical, each containing a fetus of approximately 75 mm. crown-rump length. The interior of one of the sacs, showing the fetus attached by the umbilical cord to the zonary placenta, is illustrated in Figure 1. The allantoic sac has been entered and the zonary placenta flattened out. The amnion has been removed to reveal the fetus. The cut edge of the amnion fused back to back with the wall of the allantois, is visible at the placental end of the short umbilical cord. The umbilical vessels are seen emerging from the vortex of the allantois and branching to form the placental blood vessels. A yolk sac, of digitiform shape with a somewhat bulbous tip, is seen beneath the allantoic membrane, extending from the attachment of the umbilical cord across the placental girdle to end between the allantoic membrane and the membranous chorion. Separate vitelline vessels from the umbilical cord supply it with blood. A few fine vessels extend from the margins of the placenta into the membranous chorio-allantois.

The placenta consists of a girdle which has a gap in it in the vicinity of the attachment of the umbilical cord. In this gap there are two smaller, ovoid placental masses separated from one another and from the main placental body by intervening membranous chorion.

On the interior of the placental girdle, opposite to the attachment of the umbilical cord, there is a conspicuous, dark red multilocular sac which protrudes from the surface of the placenta into the interior of the gestation sac (Fig. 1). This is evidently a variety of the well-known structures designated as hematomas, which characterize the placentas of carnivores. In this case the

sac is a "central" hematoma. Views of it cut in perpendicular planes are shown in Figures 2 and 3. There are no grossly visible "border" hematomas along the margins of the zonular placenta, corresponding to the "brown" and "green" borders of cats and dogs respectively. In addition to the large central hematoma, there are about half a dozen minute protuberances on the fetal surface of the placenta (Fig. 1). The largest of these is a pale brown elevated nodule close to the edge of the central hematoma. Two other nodules, close together in the neighborhood of the placental insertion of the umbilical cord, are dark red. Another similar minute red fleck is present on the opposite side of the placenta (near the animal's snout in the drawing) and two further elevations, of brownish color, in other places are scarcely discernible.

As revealed in cross sections of the zonary placenta, the labyrinth has a perpendicularly striated texture (Fig. 3). The thick placenta is loosely attached to the relatively thin wall of the uterus from which it separates readily. At the lateral margins of the placenta, the membranous chorion is visible.

Figure 4 is a diagram illustrating a gestation sac which has been separated and removed from the uterus. The central hematoma is shown as it appears on the basal or maternal surface of the placenta, with its orifice indicated by heavy black stippling. The relation of this orifice to the placental labyrinth will be further appreciated by reference to Figure 2.

MICROSCOPIC ANATOMY

The placental labyrinth. Seen under the microscope, the labyrinth of the chorio-allantoic placenta is typically of the carnivore type consisting of rather indistinct twisting lamellae of trophoblast which contain sinusoidal maternal capillaries and are separated by bands of pale-staining fetal stroma (Figs. 5, 7, 8). The lamellae are tortuous and apparently much branched, in these respects resembling those of the dog and ferret rather than the slender ones typical of the cat's placenta.

The individual lamellae show an arrangement of the tissue layers characteristic of an endotheliochorial placenta according to Grosser's classification. Tortuous maternal blood vessels of sinusoidal dimensions are lodged in lamellar sheets of tropho-

blast which alternate with loose-meshed fetal mesenchyme which contains delicate fetal capillaries (Figs. 7, 8). The endothelium of the maternal sinusoidal capillaries consists of greatly enlarged cells of nearly cuboidal form (Fig. 8), resembling closely the ferret and *Zorilla* and differing from the dog, bear and cat which have lower, more flattened endothelium. The endothelial cells rest upon a conspicuous basement membrane which is intensely differentiated by the periodic acid-Schiff stain (Figs. 7, 9). Unlike the cat and resembling the dog, bear, ferret and *Zorilla*, giant decidual cells are lacking between the maternal vessels. At this stage, the maternal blood vessels appear to be surrounded solely by a relatively thin layer of syncytial trophoblast, whereas cellular trophoblast is lacking (Figs. 7, 8). The trophoblast rests upon the fetal mesenchymal stroma. The fetal capillaries indent the syncytium and in numerous places follow an "intra-epithelial" course (Figs. 7, 8). The basement membranes between the trophoblast and fetal stroma and surrounding the capillaries, are so delicate that they are scarcely differentiated by the periodic acid-Schiff reagent.

From the nature of the single specimen at our disposal, the exact pattern of the maternal vascular tree cannot be determined. Nevertheless, some information can be got from the appearance of the blood vessels in the histological sections. Apparently the maternal arterioles enter, and the maternal venules leave, the placenta through the septa forming the walls of glandular compartments of the junctional zone (see below). The maternal arterioles traverse the placental labyrinth and finally branch repeatedly beneath the fetal surface (Fig. 5, arrows). The branches immediately assume the form of dilated sinusoidal channels (Fig. 5) which are the equivalent of capillaries. As these branches arise, they curve outward from the parent blood vessel and become recurrent, following a course in the opposite direction toward the base of the placenta where they join to form the efferent veins. As a result of their recurrent course near the fetal surface, many of the sinusoids encountered there are cut tangentially. The appearance of these vessels is peculiar in that the tangentially-cut endothelium lining them resembles multinucleate giant cells or small masses of syncytium (Fig. 9). The periodic acid-Schiff stain, however, reveals the true nature of these structures by demonstrating that each of them is bounded

or enclosed by a basement membrane (Fig. 7) identical and continuous with the basement membrane which is typical of all the maternal capillary sinusoids (Fig. 9).

The junctional and glandular zones. The junctional zone (Fig. 5, *jz*) at the placental base consists of a series of dilated glandular bays or compartments which are lined by epithelium and contain histotrophe (Fig. 10). Long tongues of fetal tissue, each consisting of a core of vascularized mesenchyme which is covered by a single layer of columnar trophoblastic cells, project into the glandular compartments (Fig. 12). Each of the bays seen in histological sections has a floor and lateral walls clothed by uterine epithelium (Figs. 10, 11). The floor of the compartment is usually smooth, whereas the partitions have complex outlines produced by numerous irregularly-shaped, mucosal leaves or folds, more easily illustrated than described (Fig. 11). The proximal parts of the partitions, which extend into the placenta for a considerable distance (Fig. 5), are lined by cuboidal or low columnar cells, many of which have undergone symplasmic fusion and frequently contain conspicuous vacuoles of variable sizes (Figs. 11, 12). The distal portions of the partitions exhibit an increasing amount of symplasmic transformation of the epithelium, and the ultimate branching ends of the septa appear to be disintegrating, resulting in the formation of acellular, amorphous histotrophe which fills the glandular lumens (Fig. 12).

The trophoblast covering the processes of fetal tissue projecting into the glandular compartments, consists of columnar cells which vary somewhat in height and appearance (Fig. 12). The cytoplasm contains granular material and is frequently delicately vacuolated. These cells are quite evidently engaged in absorbing and phagocytizing the histotrophe which bathes their surfaces. At the bases of the projections the columnar cells become lower and change by transition into the syncytial trophoblast of the placental labyrinth.

A decidual response with the formation of typical large decidual cells is not evident in the stroma of the junctional zone. It will be recalled that decidual cells were also absent in the labyrinth.

In the present specimen which very probably represents a stage from the second half of gestation, the glandular zone comprises

the dilated, superficial gland segments of the junctional zone (spongy zone), which have just been described, and deeper, relatively unaltered parts of the glands of the residual mucosa which extends down to the muscularis (Fig. 5, *gz*; and 10). The glandular septa penetrating the junctional zone contain the trunks of the maternal arteries and veins supplying the placental labyrinth.

Hematomas. One of the most conspicuous features of the wolverine placenta is the large central hematoma (Figs. 1, 2, 3), which consists of a multilocular sac formed by the chorionic membrane and containing extravasated maternal blood. It communicates through a gap in the placenta with the subplacental uterine mucosa (Figs. 2, 4). Its location, in relation to the placenta, most nearly resembles that in the martin, otter and badger (cf. Mossman, '37, Plate 20; Amoroso, '52, Fig. *15.12*).

The several minute elevations varying from brown to deep red, visible on the fetal surface of the placenta, are, on a miniature scale, similar in nature to the central hematoma. They consist of small sacs of folded chorionic membrane surrounding a cavity filled with varying amounts of extravasated maternal blood (Figs. 13, 14, 15, 16). Some contain deeply stained, recently extravasated blood (Fig. 16), others are somewhat older and less deeply colored (Figs. 1, 13), while the oldest are quite pale, both macroscopically and microscopically, and the blood within them has been for the most part resorbed (Fig. 14).

Although seldom evident to the naked eye, circumscribed marginal hematomas of microscopic size are occasionally present along the borders of the zonary placenta (Fig. 6). In addition, microscopic examination reveals considerable, diffuse, paraplacental bleeding, and blood resorption by the chorion (Fig. 19). These microscopic extravasations are equivalent to the macroscopically visible brown and green borders of other carnivores (cat, dog). In all of these sites where maternal blood extravasates, whether it be in the large central hematoma or in the small macroscopic and microscopic areas, the pictures of the chorionic epithelium are essentially similar. The variously infolded chorionic membrane is lined by tall, columnar, phagocytic cells which possess cytoplasm variably filled with minute vesicles, granules, disintegrating erythrocytes and pigment (Figs. 15, 18, 19). "Chorionic vesicles" of the type depicted in

the cat (Amoroso, '52) have not been encountered in the representative, but random, sections of the wolverine placenta.

The chorio-allantoic membrane. Close to the margins of the placenta, the chorio-allantoic membrane is covered by tall, columnar, phagocytic epithelium (Fig. 19). On leaving the vicinity of the placental borders, the epithelium soon passes over into a low columnar form characteristic of the membranous chorion in general (Figs. 25, 26). Membranous chorion of the latter character separates the two lesser cotyledonary placental masses from one another and from the main zonary placenta (Fig. 1).

The "rosettes" of large clear cells in the chorionic membrane of the bitch, interpreted by Amoroso ('52) as being the equivalent of the areolae of some ungulates, have not been encountered in the random sections made of the wolverine's chorion.

The yolk sac. Under the low power of the microscope, the yolk sac appears as a thin-walled cavity (Fig. 23) lined by deeply stained, possibly pseudostratified cells, containing large empty vesicles (Fig. 24). The latter perhaps represent fat which has been removed.

The umbilical cord. The umbilical cord from the umbilical ring to its placental insertion is extremely short (Fig. 1). Close to the umbilical ring it contains two umbilical arteries and one umbilical vein, an allantoic duct and a vitelline artery and vein but no vitelline duct. The allantoic duct forms a cleft lined by flattened epithelial cells. Several millimeters farther out, the umbilical vein divides into two vessels of about equal caliber (Fig. 21), and still farther out, the vitelline vessels undergo further division. The allantoic cleft increases progressively in size. The mesenchyme in the center of the cord, in the region around the umbilical vessels and the allantoic duct, is denser than the more loose-textured stroma on the periphery of the cord. The denser, central field of mesenchyme is richly vascularized by small blood vessels (Fig. 22), a condition not previously observed in a carnivore but of common occurrence in the umbilical cords of cetaceans and various ungulates (cf. Wislocki, '33).

DISCUSSION

Comparison of the placenta of the wolverine with those of other carnivores, with respect to its gross form and the presence

of the large, central hematoma, indicates that its closest placental affinities are with the martin, otter and badger (cf. Mossman, '37, pl. 20; Amoroso, '52, figs. 12, 15). According to Weber ('28) and Simpson ('45), these four animals all belong to the Mustelidae, but both authors believe that the wolverine and martin are more closely related and consequently they place these two members together in one of several subfamilies.

Comparison of the microscopic structure of the wolverine's placenta with that of other carnivores again reveals a closer affinity to other mustelids than to other fissipeds for which data are available. The structure of the chorio-allantoic placenta of the wolverine is almost identical with that of the ferret and *Zorilla*. Common to these forms is the characteristic enlargement or hypertrophy of the endothelium which lines the maternal placental capillaries, and the prominence of the basement membrane upon which the endothelial cells rest. Comparisons of the microscopic structure of other parts of the placenta and of the fetal membranes are not feasible because of the paucity of detailed information on other mustelids.

The placenta of the wolverine is an endotheliochorial one according to Grosser's classification. Actually, however, the maternal vascular channels of the labyrinth are composed of both endothelial cells and a prominent basement membrane upon which the endothelium rests. This membrane is probably a secretion of the endothelium which serves to hold the cells in place to constitute blood vessels. The unusual thickness of the basement membrane is perhaps correlated with the exceptional size and activity of the hypertrophied endothelial cells. In view of the fact that the maternal capillary sinusoids of the placental labyrinth of all carnivores possess a relatively heavy basement membrane and some also are accompanied by hypertrophied decidual cells (e.g. cat), the term "vasochorial" might well be substituted for "endotheliochorial" in designating this placental type (Wislocki, '55).

SUMMARY

The placenta of a wolverine (*Gulo gulo luscus* (Linnaeus)) is described. It is a zonary placenta with a large central hematoma which has its closest affinities to the placentas of other mustelids,

particularly the martin, otter and badger. The placental labyrinth is characterized by greatly hypertrophied endothelial cells which line the large maternal capillaries, and by the prominence of a basement membrane which completes the wall of the maternal vessels. In two other mustelids, namely the ferret and *Zorilla*, the maternal vessels are similarly constructed.

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PLATES

PLATE 1

Fig. 1. Drawing of one of the gestation sacs of the wolverine, which has been opened to show the character of the zonary placenta and the fetal membranes. The drawing is described in the text. X 1.20.

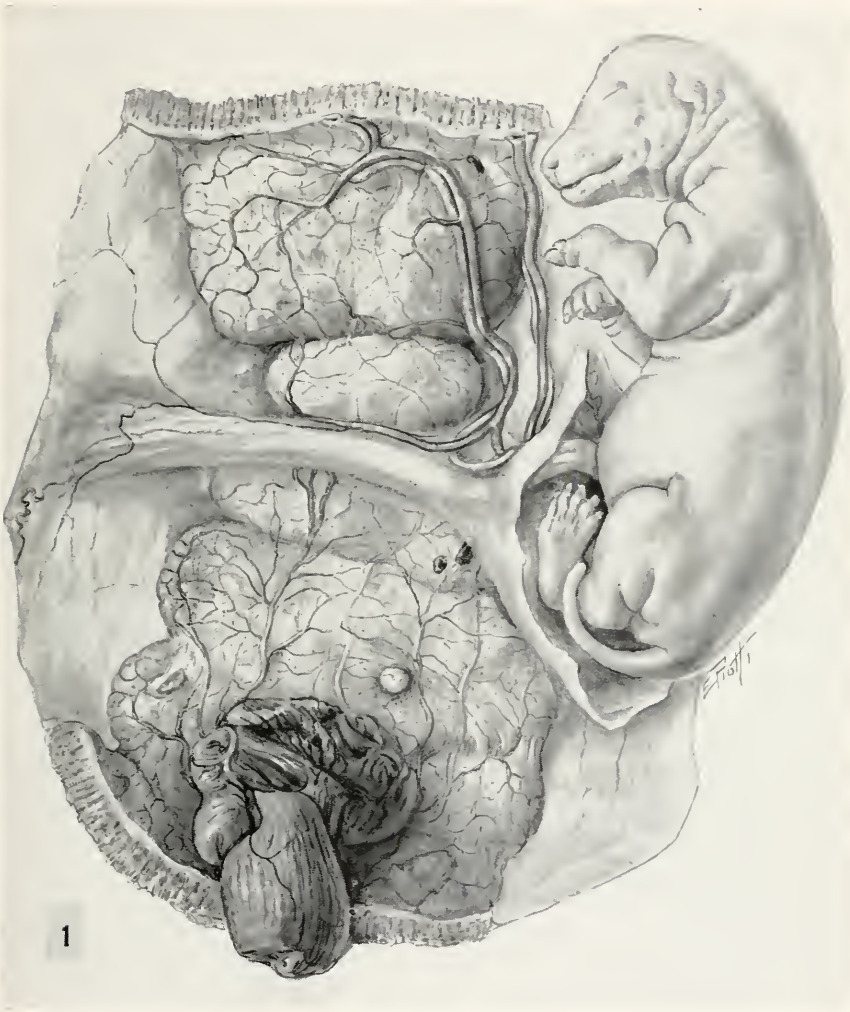


PLATE 1

PLATE 2

Figs. 2 and 3. Perpendicular, gross sections through the center and periphery of the central hematoma of the wolverine placenta. In the former, the uterine wall had separated and was removed. The orifice of the hematoma in the center of the placenta is visible in Figure 2. X 1.25.

Fig. 4. A diagram of an unopened gestation sac illustrating the position and shape of the orifice of the central hematoma. It is interesting to compare this pattern with different ones encountered in other carnivores (cf. Mossman '37, Plate 20; Amoroso '52, Fig. *15*, 12).

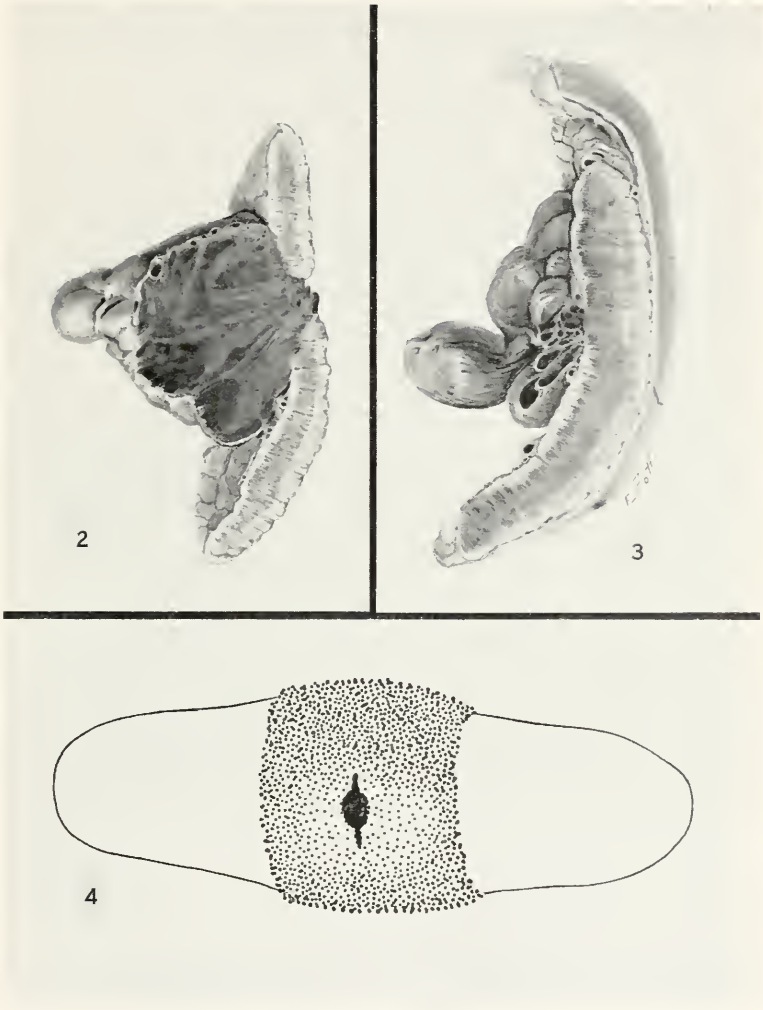


PLATE 2

PLATE 3

Fig. 5. A low power, microscopic view of the typical appearance of the zonary placenta of the wolverine. A maternal artery is visible (arrows) pursuing its way toward the fetal surface of the placental labyrinth where it branches. *Jz*, junctional zone; *gz*, deep glandular zone. X 9.

Fig. 6. The border of the wolverine's placenta, at a point where there is a small, round hematoma as well as hemotrophe and histotrophe between the membranous chorion on the one hand, and the placental labyrinth and the paraplacental junctional zone on the other hand. The field enclosed in a rectangle is shown at higher magnification in Figure 17. The uterine lumen, mucosa and musculature are visible at the very bottom of the picture. X 11.25.

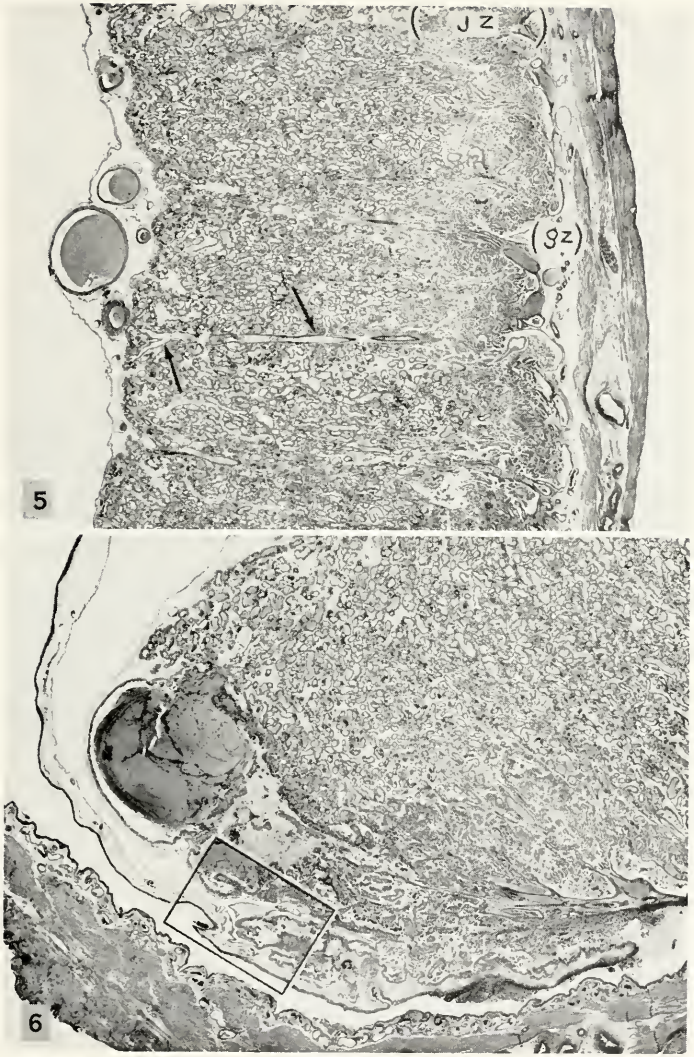


PLATE 3

PLATE 4

Fig. 7. The placental labyrinth shown at high magnification, illustrating the maternal sinusoidal capillaries lined by hypertrophied endothelial cells which rest upon a basement membrane which is intensely stained by the periodic acid-Schiff reagent. Surrounding the basement membrane the trophoblast is visible; it is syncytial in character and contains numerous "intra-epithelial" fetal capillaries. Pale, unstained, relatively acellular stroma without any basement membrane, abuts the trophoblast. X 200.

Fig. 8. A portion of the labyrinth stained by Masson's trichrome mixture. With this staining method, the endothelium lining the maternal vessels and the syncytial trophoblast is well differentiated, but the intervening basement membrane which is selectively stained by the periodic acid-Schiff reagent (Fig. 7) is entirely unstained. X 200.

Fig. 9. A portion of the labyrinth close to the fetal surface, illustrating the spurious presence of giant cells or syncytial tags, resulting from the tangential planes in which the endothelium of the recurrent maternal vessels in this region is cut. X 152.

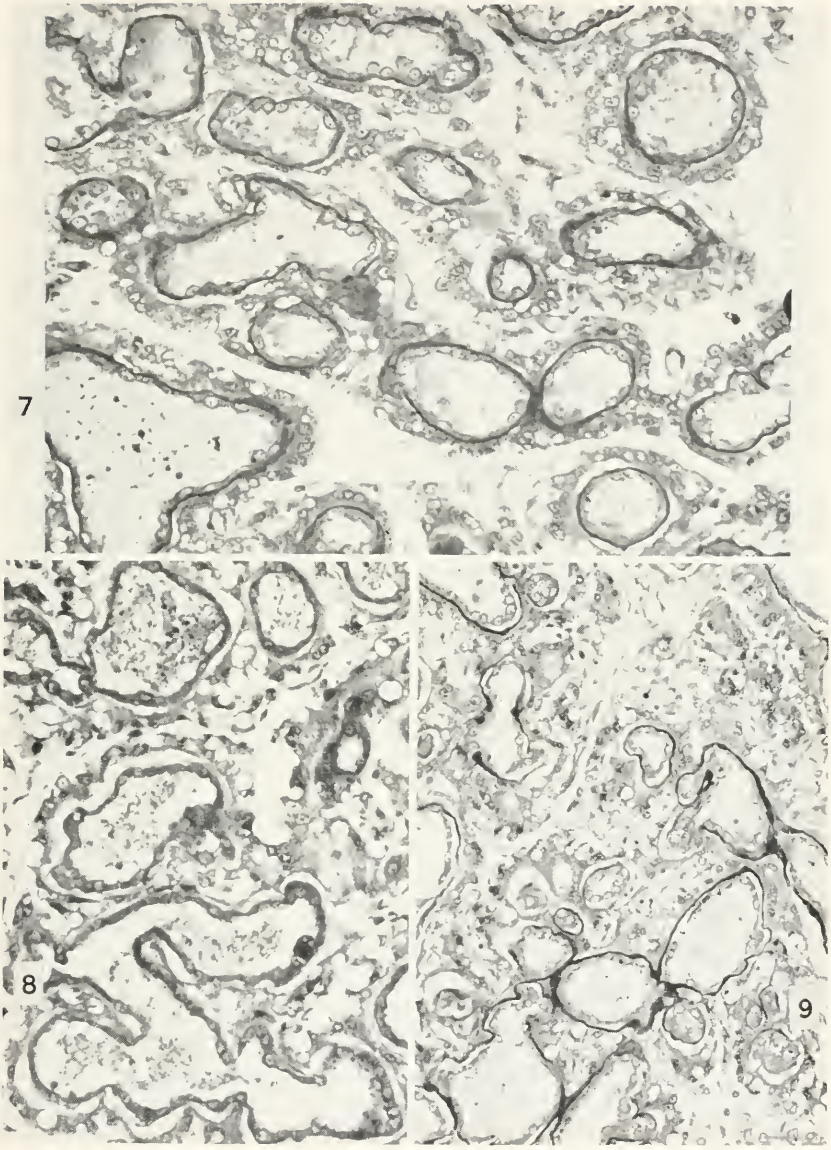


PLATE 4

PLATE 5

Fig. 10. Higher power microscopic view of the junctional and glandular zones of the wolverine's placenta. Compare with Figure 5 (*jz*, *gz*). Two entire glandular compartments and parts of two others are visible; their lumens are filled with histotrophe and the partitions between them carry the afferent and efferent placental maternal blood vessels. X 32.

Fig. 11. Illustrates a single glandular compartment with a simple floor and elaborate side walls; the walls consist of folds or leaves of stroma, covered by uterine epithelium some of which is syncytially transformed and contains vesicles. X 144.

Fig. 12. Another compartment, showing a tongue of fetal stroma covered by columnar trophoblastic cells projecting into a mass of amorphous histotrophe in the chamber. The fetal projection is flanked on its sides by folds of vesiculated maternal mucosa, some which is visibly disintegrating to form histotrophe. X 144.

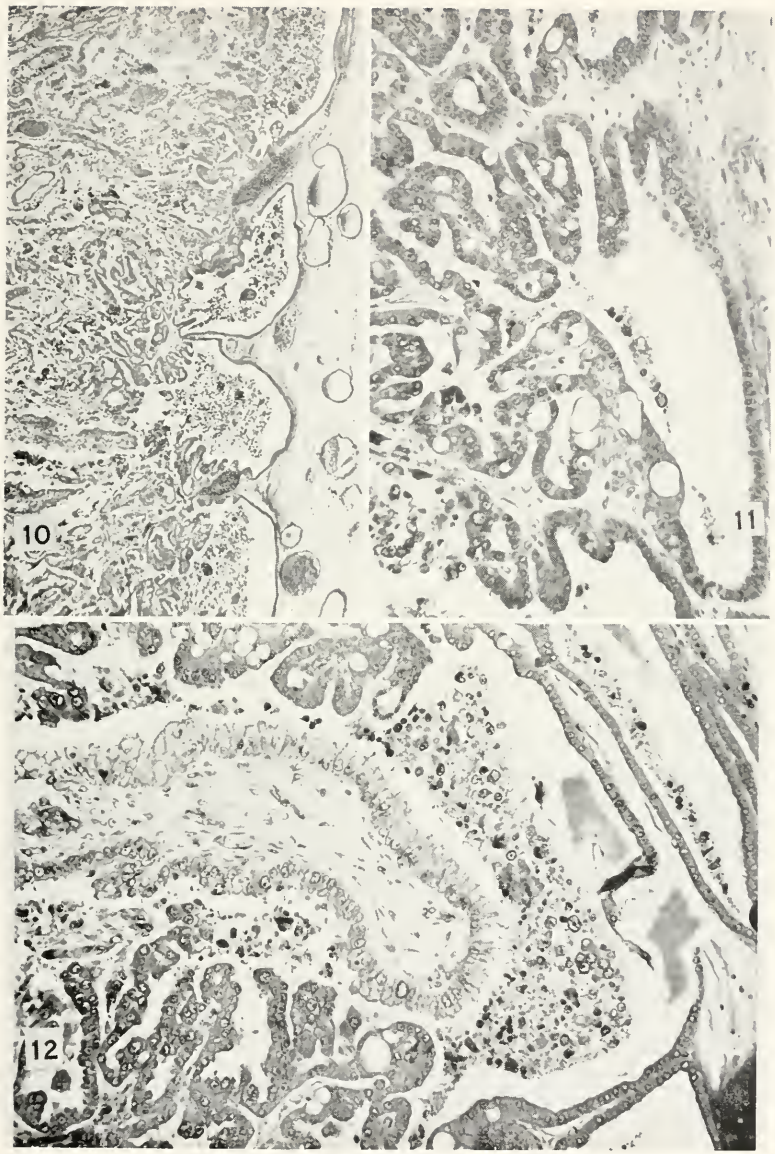


PLATE 5

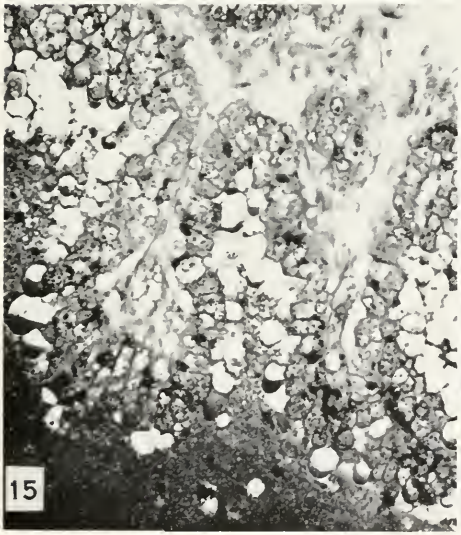
PLATE 6

Fig. 13. A section through the larger of the two minute hematomas on the internal surface of the placenta near the insertion of the umbilical cord in Figure 1. In the upper corner of the photograph there is a similar hematoma of microscopic dimensions. X 40.

Fig. 14. A section through the small, pale nodule on the internal surface of the placenta near the attachment of the large central hematoma (cf. Fig. 1). This hematoma consists primarily of elaborate infolded masses of the chorion with very little actual extravasated blood in its interior. It is interpreted as being an older hematoma in which resorption is nearly completed. X 32.

Fig. 15. A higher power view of part of the wall of the hematoma seen in Figure 13, showing folds of chorion dipping into the interior of the extravasated maternal blood. The low columnar trophoblastic cells covering the chorionic folds are phagocytic and are actively engaged in resorbing the blood. X 144.

Fig. 16. A view of an extremely minute, very recent hematoma in contact with the placental labyrinth at a site where the extravasation of blood occurred probably from neighboring maternal sinusoidal capillaries. X 160.



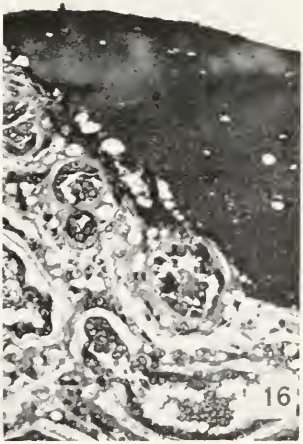


PLATE 6

PLATE 7

Fig. 17. A field at the border of the placenta, magnified from the area shown in the rectangle in Figure 6. The area in this figure delimited by a rectangle is similar to the one shown at higher magnification in Figure 18. The two arrows in this photograph indicate parts of the paraplacental membranous chorion similar to that shown at higher magnification in Figure 19. X 40.

Fig. 18. A field, similar to the one contained in the rectangle in the preceding figure, still further magnified, to show a fold of chorion dipping into a mass of extravasated maternal blood. The chorionic epithelial cells are variously laden with disintegrating blood cells, pigment, granules and vacuoles. X 144.

Fig. 19. Paraplacental membranous chorion from a site similar to the ones indicated by arrows in Figure 17, again showing the columnar chorionic epithelial cells engaged in the resorption of extravasated maternal blood. X 144.

Fig. 20. Glands in the paraplacental uterine mucosa. The low surface epithelium lining the uterine cavity is apparent above the glands. The mucosa is visible at much lower magnification in Figure 6. X 144.

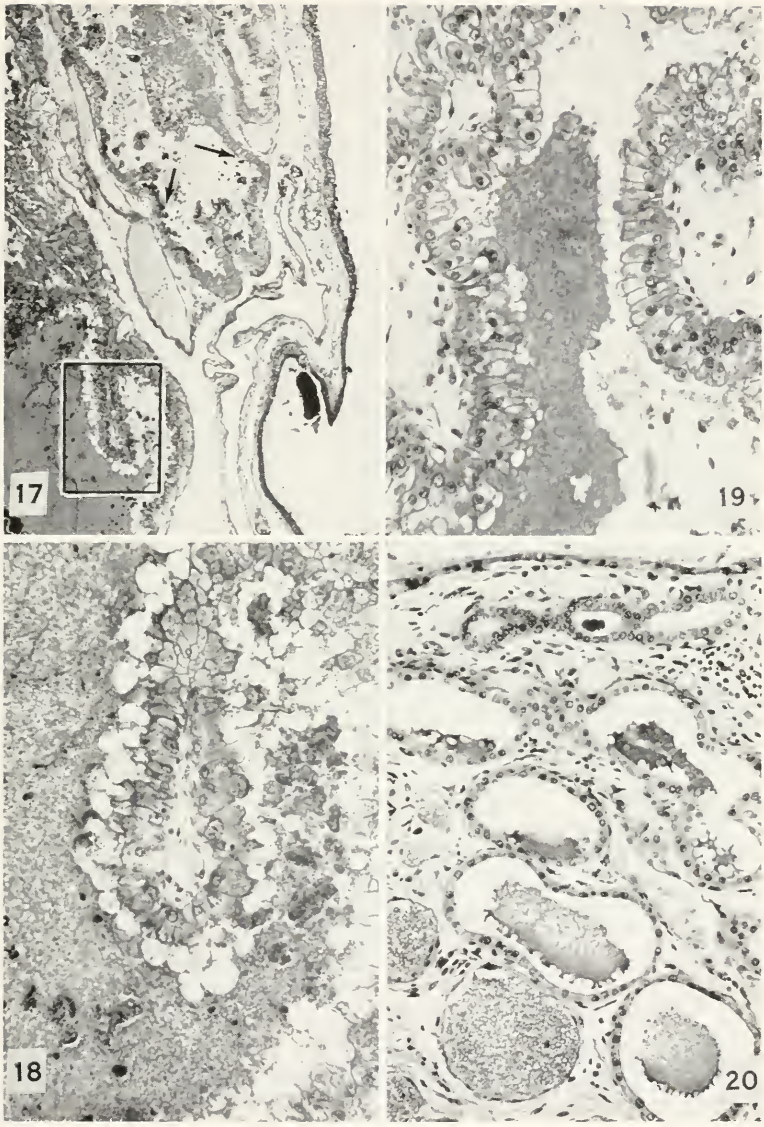


PLATE 7

PLATE 8

Fig. 21. Umbilical cord of the wolverine, half a centimeter from the umbilicus, showing paired umbilical arteries and veins with the slit-like lumen of the allantois between them and, below, the vitelline artery and vein. X 16.

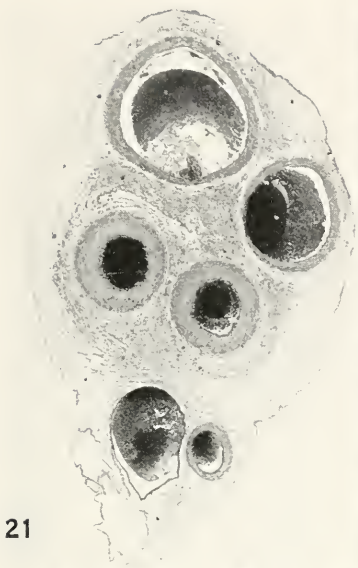
Fig. 22. A portion of the denser connective tissue in the neighborhood of the umbilical arteries, showing a rich supply of small, interstitial blood vessels which vascularize the dense, central stroma of the cord. X 160.

Fig. 23. A longitudinal section through the tip of the yolk sac, the chorionic membrane and the wall of the allantois. Abbreviations: *ys*, yolk sac; *ex*, exocoelome; *ch*, membranous chorion; *al*, allantoic cavity. X 40.

Fig. 24. The detailed appearance of a portion of the wall of the yolk sac, at high magnification. X 260.

Fig. 25. A portion of the membranous chorion overlying the yolk sac. The chorionic epithelium is lower and more inactive here than in the paraplacental region. X 260.

Fig. 26. A portion of the membranous chorion at a distance from the border of the placenta. The cells, here, are quite low and inactive. X 260.



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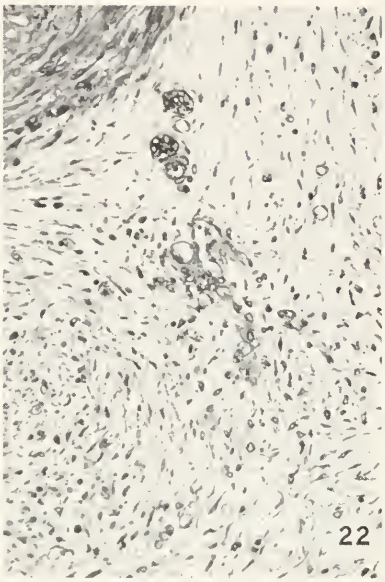

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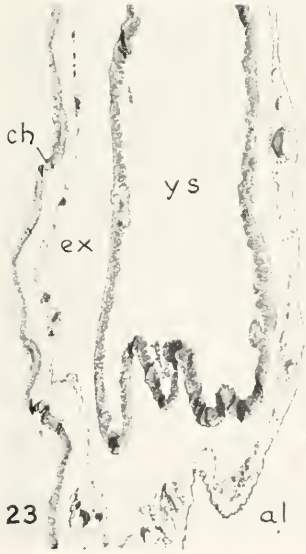

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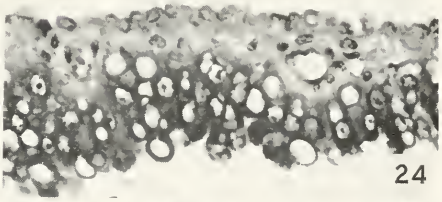

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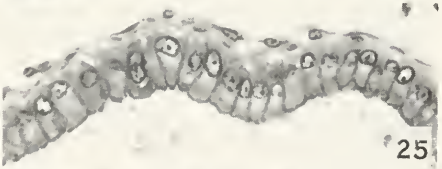

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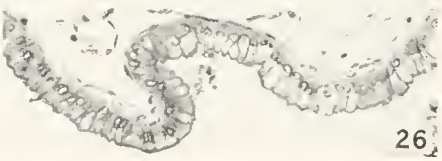

26

PLATE 8

Bulletin of the Museum of Comparative Zoology
AT HARVARD COLLEGE
Vol. 114, No. 4

THE FUNCTIONAL ANATOMY OF THE DELPHINID NOSE

by Barbara Lawrence and William E. Schevill

With Thirty Figures

CAMBRIDGE, MASS., U. S. A.
PRINTED FOR THE MUSEUM
February, 1956

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No. 4 — *The Functional Anatomy of the Delphinid Nose*[1]

By Barbara Lawrence and William E. Schevill

TABLE OF CONTENTS

	Page
Introduction	103
Materials and methods	106
General description of the nasal passage	108
Detailed description of the nasal passage	111
Outer part: blowhole and vestibular sacs	111
Constriction: tubular and connecting sacs	113
Inner part: nasal plugs and premaxillary sacs	116
Musculature of the blowhole region in *Tursiops, Stenella,* and *Delphinus*	118
Introduction	118
Pars nasalis of the maxillonasolabialis	119
Posteroexternus layer	119
Intermedius layer	121
Anteroexternus layer	122
Posterointernus layer	123
Anterointernus layer	124
Profundus layer	126
Nasal plug muscle	126
Pars labialis of the maxillonasolabialis	127
Major intrinsic muscle of the tubular sac	128
Ligament muscle	129
Minor intrinsic muscle of the tubular sac	129
The blowhole mechanism	130
Observations on its functioning	130
Anatomical explanation of function	136
Contrast with mysticetes	138
Discussion of previous work	140
Effect of hydrostatic pressure on the blowhole mechanism	147
Summary	148
Acknowledgments	149
References	150

INTRODUCTION

No description or anatomical examination can possibly give an adequate picture of a free-swimming porpoise's breathing cycle. Nor can they convey a sense of the urgent purpose behind the

[1]Contribution no. 793 from the Woods Hole Oceanographic Institution

grace and power with which it rolls to the surface and the split-second timing when it goes down. The strong rush of air as it is expelled is distinctly audible, the slight gasp of the far briefer inhalation much less so. There is a definite feeling of force behind this swift exchange of air that is never apparent in land mammals even during hurried or labored breathing. A thin puff of moisture more often than not accompanies a blow, especially when the porpoises are swimming fast and so speeding up the breathing cycle. In *Tursiops* these puffs are sometimes visible for quite a distance and frequently betray the presence of individuals that are rolling low and otherwise quite difficult to see. Occasionally the spouts are larger, spreading rapidly and mushrooming at the top, suggesting those of a humpback whale in miniature.

To a casual observer all this seems something to admire rather than to marvel at, and yet here is a mammal which is keeping its ancestral dependence on air while living its entire life in water. No wonder zoologists have long been fascinated by the adaptations arising from this most successful compromise. Of these, one of the most obvious and yet the most baffling is the breathing of the porpoise. How does it keep the air in or the water out? Investigation of this problem was begun a long time ago; as early as 1787 Hunter considered it in his "Observations on the structure and oeconomy of whales." Since then numerous workers have reported on different aspects of the blowhole region, but none of them with sufficient accuracy of detail about the structure and interrelationship of the parts involved to make possible a correct interpretation of their function. More particularly, descriptions that deal with muscle layers do not give sufficient information about the thickness of the different layers, the way in which they merge at origin or insertion, or the actual effect of their contraction. Furthermore, descriptions of the nasal sacs lack adequate detail on their position and that of their openings relative to the rest of the nasal passage. This is no reflection on the diligence of these early workers; rather it is an expression of the difficulty of distinguishing these details in any but fresh (or recently thawed) material, and of the importance of having many specimens available.

It should also be borne in mind that the focus of much of this

earlier work has been on the possible homology of structures of the blowhole region with the nasal cartilages, bones of the nose, and facial muscles of land mammals. As a result, function has, in a sense, been speculated on rather than investigated. Such speculation, not checked on living animals, has produced a conflicting mixture of fact and fancy, and even the most careful workers have failed to grasp some of the most important points.

The purpose of our work has been to unravel some of this confusion. In this paper we have attempted to explain the movement of air in the outer nasal passages, how the blowhole is opened, how it closes, and how the seal is tightened. Since such explanation will be easier to follow if the myology of the blowhole region and the interrelationships of the nasal sacs and main air passage are understood, these will be described first. We have accepted Huber's (1934, p. 131) opinion that the rostral muscles are the *pars labialis* of the *maxillonasolabialis* and that all the layers of blowhole muscle are derived from the *pars nasalis* of the *maxillonasolabialis*. We recognize six such layers, all functionally distinct, which we have called: *posteroexternus* (*pe*), *intermedius* (*i*), *anteroexternus* (*ae*), *posterointernus* (*pi*), *anterointernus* (*ai*), and *profundus* (*pr*) (Figs. 10-17). This recognition implies a more clearcut anatomical separation than actually exists. In our cross sections the only obvious division is between *pi* and *ai* (Figs. 7-9); also various layers, notably *pr*, include more than one section, but where there is no sharp distinction either in origin, insertion, or direction of fibers, such subdivisions within a layer have not been considered separately.

In studying the nasal sacs we have found that only the premaxillary sac has been consistently so identified. This term we have continued to use; otherwise we have selected appropriate descriptive names. For the sake of simplicity the descriptions are usually of the right side only; hence the sacs, although paired, are usually referred to in the singular. In keeping with the characteristic asymmetry of the skull (Fig. 1), the passage and associated sacs on the left are all less developed than those on the right.

The part of the nasal passage here considered is the distal part which lies superficial to the openings of the paired bony nares, in other words that part which lies in the soft tissues of the head between the bones of the skull and the protuberance of dense,

fatty, connective tissue above the rostrum, commonly called the *melon*.

MATERIALS AND METHODS

This paper is based on a study of both dead and living material. Detailed dissections were made of two *Tursiops truncatus*, two *Stenella plagiodon*, and one *Delphinus delphis*, all preserved by freezing. This kept the material in excellent condition even when partially thawed for dissection and then refrozen repeatedly. Cross and sagittal sections were made of two fresh adult *Tursiops*, and sagittal sections and dissections of a fetal one preserved in formalin. Dissections and comparative observations were also made on a number of *Globicephala melaena* and a single specimen of *Lagenorhynchus acutus*. Latex casts of the passage of *Stenella* and *Delphinus* were generously supplied by Dr. Henry Kritzler. In addition, the movement of air in the passage was studied by pumping air up the trachea of specimens of *Tursiops*, *Delphinus*, and *Stenella*. Most of the observations on live animals were made during the course of four visits to Marine Studios, Marineland, Florida. Here there was ample opportunity to watch, from both above and below the surface of the water, the breathing cycles of captive *Tursiops*, and less frequently of *Stenella*. Motion pictures taken at 64 frames per second show the relation of closing of the blowhole to submerging, both in groups of animals swimming at various speeds and in two different individuals idling near the surface. Other close-up pictures taken at the same speed show, in detail that the unaided eye cannot catch, how various parts of the passage move at such times.

Finally, and most important, investigations were made inside the blowhole of a live bull *Tursiops* which was kept under such observation for three days. By holding a finger in various parts of the passage (on occasion as far down as the bony nares) for extended periods between and during blows it was possible to feel both muscular and pneumatic motion. It was also possible to introduce a rubber tube and take pressure readings with a mercury manometer in different parts of the passage.

The behavior of our live animal during the three days when we had him under observation is of considerable interest in view

of a rather widely held opinion that porpoises will not tolerate tampering with the blowhole. This is probably based in part on True's observation (1891, p. 202) that stranded *Tursiops* at Hatteras "invariably showed signs of discomfort by lashing the tail violently" when he touched the blowhole. In contrast, our bull never thrashed around until in his death flurry, when he was apparently unconscious. The rest of the time he was remarkably passive, whether afloat or aground. This does not mean that he submitted with complete tranquillity to our investigations. His efforts to hold his nasal passage closed will be described later. In addition, as he lay on his side, he occasionally bent his head down away from the investigator, at the same time lifting it slightly from the deck, and sometimes opened his mouth a little as if gagging. This occurred particularly when the plugs were pulled open by hand, allowing air to escape, or when he was probed near the entrances to the tubular and connecting sacs. These occasional efforts seemed to be to avoid rather than to attack the investigator. The only time he snapped was once when we attempted to muzzle him with a rope, a precaution we gave up as unnecessary.

Irving, Scholander, and Grinnell (1941, p. 158), when working on the respiration of *Tursiops,* found them so sensitive to interference with their breathing that on occasion individuals asphyxiated themselves. These authors stated that "if a little water enters the nostril during inspiration, the animal often will not breathe again." This certainly was not the case with our animal, even when we ourselves opened his blowhole under water. Apparently neither the presence of water in the outer nasal passage nor interference with the mechanics of blowhole action are by themselves sufficiently disturbing to inhibit breathing. Some other factors must also be involved.

This individual (length 262 cm., weight about 260 kg.) was not in perfect health when caught, as shown by an extraordinary amount of flatulence and a rather bloated appearance. For this reason the mild behavior described above may not be entirely typical; it is, however, in keeping with our previous observations on these creatures.

GENERAL DESCRIPTION OF THE NASAL PASSAGE

A brief general description of the nasal passage, together with the accompanying diagrams, will help to orient the reader and enable him to understand the subsequent detailed discussion of the structure and functions of the various parts.

The inner or bony nares pass upward through the skull as a pair of simple, somewhat rounded tubes between the cranium and the rostrum (Fig. 5). Being surrounded by bone, they are not collapsible, and they lack diverticula. Paired plugs occlude their upper ends, shutting them off from the collapsible and far more complicated superficial portion of the passage which slopes more anteriorly (Fig. 2). In this paper the term "plug" refers to the mass of tissue which occludes the upper end of the bony nares, is moved by the nasal plug muscle, and has a lateral extension on the premaxillary bone.

For most of its extent the distal nasal passage is paired, being divided by a cartilaginous extension of the bony septum which separates the internal nares (Figs. 1, 5, 19, 23). The blowhole, or opening through which the passage communicates with the exterior, is single, smaller than the rest of the passage, approximately crescentic in outline when closed, and nearly round when wide open (Figs. 26-28). Essentially, the main air passage may be considered as made up of (1) a relatively fixed posterior wall sloping downward and backward from the posterior lip of the blowhole, and (2) a highly movable anterior wall comprised of the valve and the plugs, which are closely coapted to the posterior wall (Fig. 2). Bisecting the nasal passage in the midline a short distance within the blowhole is the cartilaginous septum mentioned above. Anteriorly this attaches to the wall of the passage between the plugs (Figs. 5, 19); posteriorly it attaches to the bony wall of the passage and thence curves upward and forward beneath the posterior lip (Fig. 28). The plugs are freely movable on each side of this septum, which itself limits the extent to which the passage can be drawn open anteroposteriorly.

That the apparent simplicity of a view down the open blowhole is very misleading is immediately discovered when the closed passage is investigated. Then one finds that the overlapping posterior wall fits so snugly on top of, as well as behind the anterior wall (Figs. 2, 3) that a probe thrust down must follow

a tortuous course to reach the bony nares. As a further complication there are four pairs of diverticula (Figs. 1, 20), two of which, the premaxillary and the vestibular, are broadly continuous with the passage and so widen it to a diameter far greater than that of the nares or blowhole.

The paired *premaxillary sacs* are the largest (Fig. 1) and lie immediately on top of the smooth portion of the premaxillary bone around the opening of the bony nares. They communicate with the nares internal to the plugs along the entire narial border of the premaxillae, and their superficial wall appears as an extension of the integument covering the nasal plugs (Figs. 2-4). For the most part, the premaxillary sacs are internal to the plugs, but each has a small opening at its posterolateral corner external to the plug (Fig. 22) through which air may pass into the outer passage even when the plugs are seated.

The outermost pair of sacs, the *vestibular,* are posterolateral to, and lie immediately within the lips of the blowhole (Figs. 10, 12). They are highly distensible and, when uninflated, roughly half the size of the premaxillary sacs. Like the latter they are continuous with the main passage, so that it is difficult to determine where the one begins and the other ends. Together, passage and sacs form a widened vestibular area whose inner limit is the transverse slit where the plugs pass beneath the overhanging posterior wall (Figs. 21, 22). This slit or constriction is of particular importance, as it is here that the porpoise can voluntarily tighten the closure of the passage. There is a considerable mass of tissue lying between the vestibular area and the dorsal surface of the plugs (that is to say, beneath the ventral surface of the vestibular sac) and it is here that the last two pairs of sacs, the *tubular* and the *connecting,* lie embedded. These are both true sacs in the sense that they are perfectly distinct from the main air passage and connect with it only via rather small, well-marked openings. The tubular sacs are U-shaped, lie almost horizontally in the head, and on each side surround the slitlike opening between the top of the plugs and the posterior wall (Figs. 1-3). A transverse ligament beneath the posterior limb of the tubular sac helps to stiffen the posterior wall of the passage here (Fig. 20). The connecting sacs appear as small appendices lateral and internal to the tubular sacs, into which they open (Figs. 1, 20, 22). They also lie directly over the external opening

of the premaxillary sac described above (Fig. 22), so that there is a direct passage for air from the outer margin of the premaxillary sac via the connecting sac into the tubular sac. When the tubular sac is thus inflated it pneumatically tightens the seal of the inner passage.

Surrounding the passage and sacs are six layers of blowhole muscle. Omitting the small and often poorly developed intermedius layer, the other five take origin over a wide area in the fronto-maxillary region (Fig. 23) and are found to be in two groups which insert respectively posterior and anterior to the passage, but alternate, and overlap broadly at their origin. Thus the anteroexternus partially separates the two posterior layers, while the anterior portion of the posterointernus lies between the anteroexternus and the anterointernus (Fig. 11). Where the two posterior layers are not separated by an anterior layer they tend to merge. Thus while these four layers are functionally distinct, they are by no means anatomically so throughout their entire extent. The remaining, or deepest layer, the profundus, is distinguished from the anterointernus by its more intimate connection with the rostral muscles and its insertion, chiefly in the melon (Fig. 16). The effect of these muscles on the sacs is incidental to their control of the passage; the vestibular and premaxillary sacs lack intrinsic muscles. The tubular sac is unique in being provided with a weak but rather extensive intrinsic musculature and the connecting sac is partially affected by a portion of this. The nasal plugs have their own distinct muscles.

In summary, then, the distal passage may be considered to be divided into two rather wide spaces separated by a slitlike constriction. For a more detailed description it will be convenient to deal with these three regions separately, the blowhole and vestibular sacs forming the outer part, the tubular and connecting sacs and associated parts forming the constriction, and the nasal plugs and premaxillary sacs forming the inner part. In fundamental plan the distal nasal passage is very similar in all three forms studied, so our description of *Tursiops truncatus* is equally applicable to *Stenella plagiodon* and *Delphinus delphis*. The same is true of the rather general remarks on the musculature of this region. A more thorough description of the muscle layers, as well as an account of certain slight differences between the three forms, is given below (pp. 118-129).

DETAILED DESCRIPTION OF THE NASAL PASSAGE

Outer Part: Blowhole and Vestibular Sacs

The blowhole is itself somewhat asymmetrically curved with its convexity directed backward. The anterior lip, or valve, slopes back to pass under the posterior, thus forming a slight depression which often holds a little water when the animal surfaces. The lips are thick and non-muscular, being composed of what appears to be very fibrous, less oily blubber than that which covers the rest of the animal. The posterior lip in particular is stiff and densely fibrous; in a live animal only the margin along the middle third was found to be of softer, freely movable tissue. Since the lips have no muscle attachments in them, they can move only as the underlying tissue is moved. Thus the thick, fibrous mass of the posterior lip, projecting as it does well beyond the subjacent muscles, moves relatively little, while the anterior lip or valve moves freely as part of the mass of connective tissue on which it lies. The valve in the living animal is soft and pliable to the touch, and has a well-marked margin where it passes beneath the posterior lip. It slopes rather steeply in the midline, and is continuous below and laterally with the two plugs, which are separated by the septum. On either side the passage widens into a large sac, the vestibular, which when uninflated lies lateral and somewhat posterior to the blowhole (Fig. 10). At the lips of the blowhole the smooth wall of the passage passes gradually into the more wrinkled lining of the sac with no real division between sac and passage (Fig. 13).

On the under or forward side of the passage the valve passes with no sharp boundary into the anterior fold of the vestibular sac (Figs. 2, 13, 21). This fold divides the anterior part of the sac into two unequal pockets, an inner one which is shallower anteroposteriorly, and an outer one which is much deeper and communicates directly with the blowhole opening. The fold is thickest at its medial end, and here takes origin midway between the margin of the valve and the plug. Laterally it tapers to nothing just beyond the end of the slitlike opening between the plug and the posterior wall. When the passage is closed and the sac uninflated, this fold covers the slit, thrusting against the less well developed posterior fold which forms a soft yielding mass between the stiff overhanging posterior lip and the almost

equally stiff convex inner mass that interlocks with the plug (Figs. 13, 19). This posterior fold has no real pocket beneath it and appears merely as a puckering of the wall of the uninflated sac. Various degrees of inflation change the shape of this sac in various ways, as is shown by latex casts. When it was slightly inflated, the latex reached only that part of the sac beneath the anterior fold; when strongly inflated both folds are obliterated. The vestibular sacs lie close beneath the blubber and are separated externally from the thick integument around the blowhole by the thin aponeuroses which form part of the insertion of the outermost layers of blowhole muscle, *pe, i,* and *ae* (Figs. 10, 11). Posteriorly these sacs are tightly bound to the insertion of the underlying muscles, so that here they appear thick walled, while anteriorly they are thinner walled and more loosely held in the investing tissue.

As well as enclosing the sac, the outermost layers of blowhole muscle insert internal to the dense collagenous connective tissue mass comprising the outer lips. As with the rest of the blowhole muscles, these layers are not entirely distinct from the surrounding layers, but usually merge with them at either origin or insertion so that it is extremely difficult to separate them on dissection. For this reason the pull that they exert is on an area, not a particular spot, and their contraction has a general rather than a local effect. The four outermost layers, *pe, i, ae,* and *pi* (Figs. 10-13), are chiefly concerned with opening the blowhole by drawing the valve down and forward, and by pulling upward and backward on the walls of the nasal passage which lie immediately inside the rigid posterior lip. These layers further act to hold the vestibular sac in place. Pulling on them does not stretch this sac, neither does it keep it from expanding. They do however fix this sac, determining the direction in which it expands when air is forced into it from below. Furthermore, when contracting to open the outer part of the blowhole, the outermost layers of muscle exert pressure which tends to flatten the sac, thus preventing air from being impounded there as the blowhole closes.

In opening the passage, *pe* and *pi* act chiefly on the posterior part. *Pe* draws up and back the outer wall of the vestibular sac and that portion of the passage which lies just inside the posterior

lip. The tendinous insertion of *pi* (Fig. 14) curves over the nasal bones to a deeper attachment, chiefly in the slightly developed posterior fold of the vestibular sac and the tissue ventral to this, including the outer side of the tubular sac. Posteriorly *pe* and *pi* are not separated by other layers, and at their insertion are not truly distinct. Here their thick tendinous mass fills the space between the nasal bones and the nasal passage, and, where the vestibular sac lies on top of this mass, it is closely attached to it.

While *pe* and *pi* have their main mass posteriorly and control the posterior part of the nasal passage, *ae* has its main mass anteriorly and acts on the anterior part of the passage (Figs. 11, 13). It is largely responsible for depressing the valve by pulling the tissue beneath it anteroventrally, and further helps to open the nasal passage by pulling the well-developed anterior fold of the vestibular sac anterolaterally as well as ventrally, away from its position on the top of the slitlike opening of the passage above the plugs. In addition, *ae* anchors the underside of the vestibular sac, so that when inflated it has to expand on top of *ae*. *Pe*, *ae*, and *pi* are all separated from the melon and the pars labialis of the maxillonasolabialis by the collagenous connective tissue in which the posterior, external fibers of this latter muscle end (Figs. 11, 13). Layer *i* is very thin with no bony attachments, and makes a connection, otherwise lacking, between *pe* and *ae* and the melon (Fig. 11).

Constriction: Tubular and Connecting Sacs

Although, for convenience of description, the nasal passage is here divided into three, there is no real separation between these regions. As noted above the innermost portion of *pi* attaches on the tubular sac, and the slitlike opening at the inner end of the vestibular area also marks the outer end of the constricted area. Surrounding the slitlike opening on each side and more or less embedded in fatty connective tissue are the tubular sacs, which are paired, asymmetrical, and U-shaped (Figs. 15, 22). The posterior portion of each of these lies between the nasal bones and this opening. Together with its surrounding muscles, the blowhole ligament, and connective tissue, this portion of the sac forms a transverse, convex band in the posterior wall of the

passage, which, when the passage is closed, fits into a concavity on the superficial surface of each plug (Fig. 3). The smaller anterior portion of the sac lies beneath the valve. The tubular sacs each open downwards into the nasal passage through a more or less horizontal slot in the posterior part near the bend of the U. This slot slopes posteroventrally for a very short distance to open immediately dorsal to each plug and slightly anterior to where the plug lies against the posterior wall of the bony nares (Figs. 1, 3, 17, 20, 22). Thus the only entrance to the sac is from below, and when the passage is closed this opening is external to the plugs. Medially, the opening lies very close to the bony wall of the naris; laterally, owing to the slope of the skull, the opening lies a slight distance in front of this wall.

Lateral to the tubular sac and deeper, lies a small diverticulum, the connecting sac (Figs. 1, 16, 20), which is separated from the former by a deep section of the major intrinsic muscle of the tubular sac, which is here poorly developed and liberally streaked with collagenous connective tissue; the connecting sac opens downward into the nasal passage near the posterolateral corner of the nasal plug, and upward into the end of the ventral opening of the tubular sac (Figs. 20, 22). The opening of the connecting sac into the nasal passage lies over the lateral opening of the premaxillary sac. It is bounded anteriorly by the blowhole ligament (Fig. 20), to which its ventral surface is closely attached, so that its entrance does not collapse when the passage is closed. This makes it easily possible, even when the passage is closed, for air passing out of the posterolateral corner of the premaxillary sac external to the plug to enter the connecting sac, and difficult for it to go elsewhere. The blowhole ligament passes from the premaxillary bone to the lateral extremity of the slit-like opening above the plugs, where in some specimens it is stiffened by a small band of cartilage; from here a few fibers form a transverse band immediately posterior to this opening and end in the tissue beside the septum. This ligament is a very important structure that strongly anchors the commissure of the opening and makes taut the posterior wall above the plugs. Moreover it is slightly elastic, so that contraction of *pi* can lift it away from the dorsal surface of the plug, but when this layer is relaxed the ligament snaps back into place. Immediately beneath it and with similar orientation is a poorly developed slip of the major in-

trinsic muscle, the ligament muscle; together they separate the connecting sac from the lateral edge (Figs. 16, 20) of the premaxillary sac.

Of the layers of blowhole muscle, three (*pi*, *ai*, and *pr*) are more or less associated with this middle region of the distal nasal passage (Figs. 13-16). *Pi*, as described earlier, acts to some degree on the outer part of the passage and has, externally, a strongly tendinous insertion with anteriorly directed fibers (Fig. 13). Deeper dissection shows the direction of the fibers to be progressively less horizontal, more anteroventral, and where the innermost layers attach on the tubular sac there is no intervening mass of tendon (Fig. 14).

Ai and *pr* have in common a rather coarse and tendinous structure, attachments in front of the nasal passage, and an intimate connection with the pars labialis. *Ai* has as its primary function to help *ae* depress the valve by drawing the tissue beneath it downward and forward. The main mass of *ai* is anterior, and the thin aponeuroses which form the insertion of the outermost layers lie in part on top of the anterior part of the tubular sac (Fig. 14). Insertion of the deeper portion is more via slender strands than aponeuroses, and is largely anterior to the tubular sac, which is firmly attached to it (Fig. 15). As the posterodorsal border of this muscle tends to follow the edge of the premaxilla, and as in this region its fibers course anteroventrally as well as medially, its contraction would not put pressure on the lateral corner of the nasal plug, although it would do so on the anterior part of the connecting sac.

Pr is made up of many subdivisions which are impossible to separate fully, but which show a progressive change in the direction of the fibers (Figs. 16, 17) from the outermost, which take about the same direction as those of *ai*, to the innermost, which are nearly horizontal. At their origin and, except for the innermost layers, at their insertion, the fibers of *pr* are continuous with those of the pars labialis of the rostrum. The innermost layers curve inward anterior to the nasal plug muscle and between it and the melon (Fig. 18). Functionally also, the two muscles work together to draw the mass of the melon down towards the skull and back against the premaxillary sacs, thus providing a relatively rigid backing for the nasal plug muscles, and putting pressure on these sacs.

In addition to these layers of blowhole muscle, there are also associated with the tubular sac, and to a certain extent also with the connecting sac, two pale, ill-defined muscles, the major and minor intrinsic muscles of the tubular sac (Figs. 15, 16) and a small slip of the former here called the ligament muscle; these are exceedingly hard to separate from the surrounding connective tissue. The *major intrinsic muscle* attaches to the posterior and underside of the posterior part of the tubular sac, and runs posterolaterally to end in the fatty connective tissue between this sac and the skull; near the bend of the tubular sac the fibers change direction as shown (Fig. 15), and pass to the underside of the sac. Anteriorly the muscle fibers become much more sparse; the outer ones insert along the anterior margin of the tubular sac and at their origin are hard to distinguish from the long slender threads of the tendinous insertion of *ai* (Fig. 15). This combination of scattered muscle fibers and fatty collagenous connective tissue is rather thick in this region, and, as well as attaching to the underside of the tubular sac, attaches also to the top of the connecting sac. Closely connected with the anterior part of the major intrinsic muscle is the *ligament muscle*, which has its origin in the fascia beneath the blowhole ligament and inserts in part in the tissue at the commissure of the passage and in part in the wall of the premaxillary sac where this attaches external to the plugs. Wrapping around the anterior part of the posterior half of the tubular sac is a similarly pale and even less well developed muscle, the *minor intrinsic* (Fig. 15), which arises in the fatty collagenous tissue between the sac and the nasal passage, and passes posterodorsally to insert beneath, on the anterior edge, and on top of this part of the sac. Apparently the function of both the major and minor intrinsic muscles is to help anchor and hold open the tubular sac. The ligament muscle probably helps also to hold open the external opening of the premaxillary sac.

Inner Part: Nasal Plugs and Premaxillary Sacs

The above described, non-rigid parts of the passage are shut off from the permanently open bony nares by paired plugs attached in the midline to a cartilaginous septum which divides the passage and limits the extent to which it can be pulled open (Figs. 19, 27, 28). The openings of the nares face anterosuperiorly so that

the plugs lie obliquely across the passage on each side of the septum (Figs. 2, 3). This septum is roughly triangular, with the hind margin extending along the upper end of the bony septum, then up the bony wall of the nares and finally curving forward under the posterior lip; and with the front margin rising more nearly vertically between the two plugs (Figs. 5, 19). At the anterior edge of the bony nares the lower margin of each plug is closely attached to the septum; this then is the pivot on which the rest of the mass works as it is drawn anteroventrally to open the passage. At this point the plugs meet the septum almost at right angles and form a very small posterior projection on each side of it. As they slope back across the passage they project increasingly far, till at their upper edge septum and plugs meet at the apex of a V (Figs. 5, 22). This allows the posterior part of the plugs to be freely movable along each side of the septum.

The position and extent of the premaxillary sacs is marked on the skull by a characteristic smooth area on the premaxillae surrounding the bony nares. Lying as they do beneath the plugs, these sacs communicate with the inner passage along the narial borders of the premaxillae (Figs. 1, 23). Their anterior portion forms a well-defined pocket with no other openings. Along its peripheral margin the sac attaches to the premaxilla and then along the maxillo-premaxillary suture where its black wall is visible when *pr* is cut away (Figs. 16, 18, 19). Medially the sac wall is continuous with the integument of the under surface of the plugs, except posteriorly where it attaches on top of the liplike extension of the plug instead of being continuous with its margin. This forms an opening to the sac external to the plugs (Fig. 22) where air which has passed into the premaxillary sac along the bony margins of the nares can pass outward into the upper nasal passage without unseating the plugs. This opening lies close beneath the opening of the connecting sac, so that when the main passage is closed, air from here reaches first the connecting sac and then the tubular sac (Fig. 20).

The dorsal surface of each plug is not horizontal, but slopes somewhat ventrolaterally and is characteristically smooth-skinned and concave. Fitting into this concavity is the above-described convexity formed by the posterior limb of the tubular sac, the blowhole ligament, and the mass of tissue associated with them (Fig. 3). On their under surface, posteriorly, the plugs are

roughly oval and somewhat protuberant. The mass of collagenous connective tissue of which they are formed is thickest here where the plugs lie snugly against the margins of the opening of the bony nares. Anteroventrally this cushion becomes thinner and passes without a well-defined boundary into the membranous external wall of the premaxillary sac (Fig. 19). Laterally the cushion of the plugs is more sharply set off from the liplike extension which lies on top of the premaxillary bone beneath the connecting sac (Figs. 18, 19). The paired openings of the bony nares are made oval by a tough membrane (Fig. 19) stretched across the angle where the maxilla and mesethmoid meet, that is to say, the posterolateral corner. This membrane is so situated that air from below cannot lift the liplike extension of the plug up against the opening of the tubular sac, while it can press the medial part of the plug more tightly against the interlocking mass of the posterior lip.

The paired nasal plug muscles themselves are distinct from the layers of the pars nasalis and from the pars labialis. They take origin in part lateral but chiefly anterior to the premaxillary sacs and course posteromedially to a diffuse insertion in the collagenous connective tissue of the cushion of the plug, and are themselves heavily streaked with collagenous connective tissue (Figs. 3, 19). Their contraction draws the plugs down and forward.

MUSCULATURE OF THE BLOWHOLE REGION IN *TURSIOPS*, *STENELLA*, AND *DELPHINUS*

Introduction

Before describing in detail the various layers of blowhole muscle (Huber's pars nasalis of the maxillonasolabialis), a few general remarks may be helpful. The layers are in thin sheets. Those controlling the posterior part of the passage are thickest posteriorly, hard to distinguish from each other in this region, and, at their origin, extend less far forward. Obviously, also, because of the shape of the passage they are the more external layers. Those controlling the anterior part of the passage are correspondingly thickest anteriorly where they tend to merge with one another, and extend less far posteriorly. Thin layers of

loose connective tissue separate more layers of muscle fibers than seem to be functionally distinct. Of the distinct layers the outermost are inserted via aponeuroses of varying thickness while the inner ones have a more tendinous insertion, the individual strands often being discrete instead of in bundles. It will also be seen from the figures that while the actual muscle fibers of the superficial layers extend at least as far as the vestibular sac before being replaced by aponeuroses, the muscle fibers of the deep layers become increasingly shorter as the passage widens. Other interesting features are the way in which the anterior and posterior layers alternate with each other, as well as the fanning out of certain layers. The effect of this rather intricate arrangement is to balance the forces pulling in various directions, so that while the passage is being opened it is also anchored against too strong a pull in any one direction.

The three forms studied resembled each other closely. Such differences as were found were chiefly in the position and degree of development of minor subdivisions of the various layers. For this reason *Tursiops* is discussed in detail and only the ways in which the others differ are noted. Some of these differences may be merely individual variation; the number of specimens dissected is not sufficient to show how great this is; and the bilateral asymmetry is considerable.

It should also be noted that the way in which the bones in this region overlap varies within a species so that, while the region of attachment of each layer remains fairly constant, the actual bones involved may vary. For instance, in the specimen figured the frontal does not intervene broadly between the occipital and the nasals, while in others it does.

Pars Nasalis of the Maxillonasolabialis

Posteroexternus layer of the pars nasalis of the maxillonasolabialis

Tursiops (*pe;* Figs. 10-12, 23)

This is the outermost of the blowhole muscles and takes origin in a broadly continuous sheet over a wide area. Posteriorly it is thick, and at its posteromedial edge along the raised margin of the naso-frontal bones it is hard to distinguish from *pi* which lies

beneath it. Anteriorly it tapers to a very thin sheet which is difficult to separate from *i*. At its insertion the converging fibers overlap in a way that makes the muscle appear double. A very thin inner section is separable only with difficulty from the main mass of the muscle and intimately connected with *ae* where the two meet.

Origin: On the maxilla, frontal, and occipital; where the occipital forms a crest along the occipitofrontal suture, *pe* attaches beneath it. Anteriorly *pe* is difficult to separate from *ae*.

Insertion: Posterior to the blowhole opening. The anterior part of the muscle has dorsally directed fibers which pass in a very thin aponeurosis across the vestibular sac and then continue superficial to the posterior part of the muscle to attach in the denser collagenous connective tissue of the wall of the nasal passage just internal to the stiffened, crescentic posterior lip. The posterior part of the muscle has fibers that run anteromedially, passing deep to the anterior part to insert in the collagenous connective tissue of the posterior wall of the nasal passage. It also inserts on the vestibular sac. When this is flattened and uninflated these attachments are along the posteromedial margin and merge with similar attachments of the posterior part of *ae*. The anterior part of *pe* is intimately connected with the loose connective tissue investing the vestibular sac, chiefly over its superficial surface. These attachments of *pe* on the vestibular sac merge anteriorly with similar attachments of *i* which here lies internal to it.

Function: The posterior part when contracted pulls back the posterior wall of the blowhole and the movable, medial part of the posterior lip; more laterally it draws up and back the posterior wall of the vestibular sac, including its posterior fold. The attachments on top of and along the posteromedial margin of the vestibular sac are such that contraction of this layer does not stretch the sac, while the aponeuroses which lie on top of the sac help to flatten it when the blowhole opens.

Delphinus

Resembles *Tursiops* closely except that the anterior portion of *pe* has its origin slightly more posteriorly and the insertion of this part forms a more conspicuous transverse band across the insertion of the posterior part. Also the anterior margin of *pe*

and posterior margin of *i* are more distinct.

Stenella

The fibers of the anterior and posterior sections do not cross at their insertions as in *Tursiops* and *Delphinus*, but converge evenly. In *Stenella*, *pe* differs further in having a more distinct inner layer which has, however, the same origin and insertion as the outer layer and so is here considered as part of *pe*.

Intermedius layer of the pars nasalis of the maxillonasolabialis

Tursiops (*i;* Figs. 10, 11)

This is a small, not very distinct, anterodorsally directed muscle which lies between *pe* and *ae*.

Origin: Beneath *pe* from the connective tissue sheath of *ae*.

Insertion: In the fatty, fibrous mass of the melon and on the anterior part of the superior surface of the vestibular sac (Figs. 10, 11). Its insertion, via a thin aponeurosis, on the vestibular sac lies beneath and merges with that of the most anterior part of *pe*. In front of the vestibular sac its fibers merge with those of *ae* to attach via strong aponeuroses in the connective tissue of the valve at the commissure of the blowhole, as well as beneath the valve more medially. Those anteriormost fibers which insert in the melon are quite distinct from the underlying layers, and it is this distinctness which is the principal reason for recognizing this layer as a separate one.

Function: Forms the main connection between the outer layers of blowhole muscle and the melon.

Delphinus

Layer *i* is broader and better developed than in the other two genera, with fibers directed more anteriorly. Posteriorly a few fibers originate directly from the maxilla, and the attachments of this layer on the superficial aspect of the vestibular sac extend further posteriorly and nearer the ventral margin of the uninflated sac.

Stenella

Differs chiefly in having the fibers directed slightly more dorsally and less anteriorly than in *Tursiops,* so that their insertion in the melon is nearer the blowhole; further, part of the origin is from the maxilla via a very thin aponeurosis.

Anteroexternus layer of the pars nasalis of the maxillonasolabialis

Tursiops (*ae;* Figs. 10-13, 23)

While the main mass of this muscle is anterior, it is entirely distinct from the melon and the pars labialis of the maxillonasolabialis, from which it is separated by a thin fibrous sheet.

Origin: Chiefly on maxilla, with a thin extension onto the frontal. While at its origin it is largely distinct from *pe*, it tapers posteriorly to a thin sheet of connective tissue which is difficult to separate from this layer. Anteriorly its connections with the two layers internal to it are equally close. Here at its insertion on the maxilla it merges with *pi* and anterior to this a few fibers are inseparable from *ai*.

Insertion: Via strong aponeuroses chiefly in the dense, collagenous connective tissue beneath the valve from the commissure of the blowhole almost to the midline, and continuously from this onto the anterior fold of the vestibular sac. In addition, thin aponeuroses attach over the vestibular sac. Anteriorly these are distinct; posteriorly they merge with similar layers of *pe*. In effect, *pe*, *i*, and *ae* enclose the vestibular sac in thin aponeuroses, *pe* and *i* attaching more to the margin with only a few sheets passing to the outer and inner sides. As described above, the insertion of *i* merges in part with that of *ae;* the insertions of *ae* and *pi* are, however, entirely distinct.

Function: This layer controls quite a large area. Contraction depresses the valve by pulling the tissue beneath it and as far internally as the beginning of the separation of the plugs; it also draws the anterior fold of the vestibular sac forward, laterally, and down. Counteracting this forward pull on the vestibular sac, the posterior, less elastic part of the layer helps to hold the sac in place. The internal attachments of this muscle are such that the sac must expand on top of, rather than underneath it.

Delphinus

In general *ae* resembles that of *Tursiops*. It differs in having a very thin but distinct inner layer attaching to the underside of the vestibular sac and merging with *pi* posteriorly. This in *Tursiops* is probably represented by a tenuous layer of connective tissue.

Stenella

Here there seems to be a more obvious separation of *ae* into two parts, the second being posterior as well as internal to the first. Together they perform the function of *ae* in *Tursiops* and their joint origins and insertions differ only in a more extensive attachment of the posterior part on the posterior margin of the vestibular sac and in a closer connection with *pi* at the maxillary origin.

Posterointernus layer of the pars nasalis of the maxillonasolabialis

Tursiops (*pi;* Figs. 11-14, 23)

Although this layer has a very wide origin, its greatest development is posterior. The actual musele fibers are peripheral; beneath the vestibular sac and superficial to the plugs these fibers end in and are replaced by thin aponeuroses.

Origin: On the maxilla and frontal with a small area on the occipital. At its origin it is thickest posteriorly, covering a much wider area than the outer layers. In the region where the maxillofrontal suture bends upward it tapers to a thin layer without muscle fibers. Anteriorly, it becomes more muscular and again somewhat thicker. At its anteriormost attachment on the maxilla it is hard to separate from *ai;* it also merges with *ae*. From this margin thin layers of tissue merge with the strands at the end of the pars labialis of the maxillonasolabialis. Posteriorly where it arises beneath *pe* it is distinct from this layer.

Insertion: Its principal insertion is internal to *pe* in the posterior wall of the nasal passage beneath the vestibular sac, as well as in the shallow posterior fold of the sac. This insertion is via a thick, shiny, tendinous mass, whose fibers trend anteroventrally to fill the space between the nasal bones and the passage, and which is closely attached to the underside of the vestibular sac, particularly posterior to the slitlike opening of the main passage between the dorsal surface of the plugs and the posterior wall. Where the tendinous insertion of *pe* lies on top of that of *pi*, the two are difficult to separate. Deeper dissection shows the fibers of *pi* to slope progressively more ventrally, less anteriorly, to a less tendinous insertion on the tubular sac. Additional lesser attachments are via aponeuroses to the underside of the vestibular

sac in the region lateral and slightly anterior to the slitlike opening between the dorsal surface of the plugs and the posterior wall; other similar sheets extend forward between *ae* and *ai* to merge in the melon with the insertion of the pars labialis of the maxillonasolabialis. These attachments are of very secondary importance, and most of the muscle, even the anterior part, converges to insert behind the nasal passage, as described above.

Function: Contraction of this muscle helps *pe* to draw back the posterior fold of the vestibular sac; it also (and this is very important) helps to open the slitlike passage between the posterior wall and the dorsal surface of the plugs. This is accomplished by pulling up and back the convex mass including the blowhole ligament and the tubular sac which lies in the concavity of the plugs. The anterior insertions of this layer help to counteract this powerful backward pull and, together with *ae*, prevent the contraction of the very strong posterior section from distorting the entire passage. A further effect of the contraction of *pi* is to put pressure on the posterior part of the tubular sac, which would force out air trapped here.

Delphinus

Differs from *Tursiops* and *Stenella* in having the anterior attachments reduced to a very few poorly differentiated strands which pass to the posterolateral commissure of the nasal passage beneath the vestibular sac. Further, at its origin it tapers gradually from a thick posterior portion to a thin anterior, but lacks a pronounced thinning midway. At its origin anteriorly it is also distinct from *ae*, though it merges with *ai*.

Stenella

Two very distinct parts of this layer were found, the external of which differs from *Tursiops* and *Delphinus* in having the anterior fibers directed more dorsally and with better developed attachments anterior to the nasal passage. The thicker internal layer controls the posterior wall of the passage beneath the vestibular sac.

Anterointernus layer of the pars nasalis of the maxillonasolabialis

Tursiops (*ai:* Figs. 11, 13-15, 23)

This is a very thin tendinous layer, slightly thicker anteriorly,

which could possibly be considered as merely a very distinct part of *pr.* Along its anterior and posterior margins it is closely connected with *pr,* but otherwise the two layers of muscle fibers are quite distinct, the boundary being marked by strong shining tendons connected by thinner sheets of connective tissue. The actual muscle fibers are chiefly lateral to the maxillo-premaxillary suture, the posterodorsal ones following around this rim.

Origin: On the maxilla and frontal internal to *pi* and anteriorly internal to *ae* as well. A few of the anteriormost fibers merge with *pi.* At its origin anteriorly it merges with the pars labialis of the maxillonasolabialis so that the two are impossible to separate.

Insertion: Anterior to the nasal passage in the dense collagenous connective tissue beneath and lateral to the valve. The strong transverse sheet of its insertion shows many slender tendons which branch and vanish and are hard to separate from similar insertions of *pr.* In relation to the tubular sac, to which it is firmly attached, the insertion is in tissue which lies in part on top of this sac, in part anterior to it. The fibers converge towards this area from their rather wide origin, the most posterior ones assuming an anteroventral direction to do so. As the main mass passes dorsally anterior to the slitlike opening between the dorsal surface of the plugs and the posterior wall, it lies on top of the tubular sac; laterally it only partly covers this sac. At its insertion anterior to the tubular sac, some of its fibers are hard to distinguish from those of the major intrinsic muscle of the tubular sac.

Function: Helps depress the valve by pulling downward and forward on the tissue beneath it, and puts pressure on the anterior part of the tubular sac.

Delphinus

Differs in having a better developed posterior section, with origin extending as far as the nasal bones, and some of its insertion via thin aponeuroses in the area posterolateral to the slitlike opening of the passage between the plugs and the posterior wall. Anteriorly it also differs in being more closely connected with *ae* at its origin.

Stenella

This layer does not differ significantly from that of *Tursiops.*

Profundus layer of the pars nasalis of the maxillonasolabialis

Tursiops (*pr;* Figs. 16, 17, 18, 23)

This muscle is composed of a number of sections which are separated with difficulty. The fibers of the outermost ones have approximately the same direction as those of *ai.* The deeper ones are directed progressively more anteriorly (less dorsally). The outer layers of *pr* are inseparable both at their origin and their insertion from the pars labialis of the maxillonasolabialis. The innermost layers are distinct at their insertions only. This muscle is the most tendinous of all the blowhole muscles with numerous small bipinnate sections. The tendons of these sections converge to form strong strands which divide again to insert in the melon.

Origin: Beneath *ai.* The inner layers arise on the maxilla and from the strong, thick, lateral margin of the premaxillary sac.

Insertion: In the fibrous fatty mass of the melon anterior to the tubular sac and its major intrinsic muscle. The innermost layer forms a more or less transverse band across the attachment of the nasal plug muscle, separating it from the pars labialis of the maxillonasolabialis.

Function: Draws the melon strongly down towards the premaxilla. This flattens the premaxillary sac and also makes a firm mass towards which the nasal plug muscles can pull. The band across the base of the nasal plug muscle helps to limit its motion here.

Delphinus

Does not differ significantly from *Tursiops.*

Stenella

Does not differ significantly from *Tursiops.*

Nasal Plug Muscle

Tursiops (Figs. 2-4, 8, 9, 19, 23)

This muscle is entirely independent of the six layers of blowhole muscle. It is abundantly streaked with collagenous connective tissue which becomes more and more concentrated until it finally replaces the muscle entirely in the pad of the plugs. From its origin, it takes a posteromedial direction.

Origin: Chiefly on the premaxilla anterior to the premaxillary sac, with a few fibers arising in the connective tissue band along the margin of the premaxilla lateral to the sac.

Insertion: In the dense collagenous connective tissue of the plugs.

Function: To withdraw the plugs from the openings of the bony nares. The diagonal direction of the fibers and their strong medial insertion makes the dorsomedial parts of the plugs the most movable. This motion can be seen in photographs taken at 64 frames per second.

Delphinus

As in *Tursiops.*

Stenella

As in *Tursiops.*

Pars Labialis of the Maxillonasolabialis

Tursiops (Figs. 11-13, 16-17, 18, 23, 25)

This large muscle lies anterior to the layers of blowhole muscle and the nasal plug muscle. It is very coarse and mixed with numerous heavy collagenous connective tissue fibers, especially externally. Here the muscle fibers are directed laterally and posterolaterally; deeper dissection shows a gradual shift in direction, first to more vertical and then to anteromedial. The muscles on each side, although for the most part separate, are connected by a few fibers anteriorly, and behind this by a poorly developed transverse band of connective tissue beneath the melon.

Origin: From the maxilla; on the premaxilla it merges gradually with the tissue beneath the melon. The origin of the deeper portions is not distinct posteriorly from that of the deeper layers of blowhole muscle.

Insertion: Externally the more ventral fibers end in the fibrous connective tissue between the upper lip and the melon, the more dorsal in the melon itself and in the fibrous sheet of tissue separating the melon from the outer layers of blowhole muscle. Internally the fibers insert in the melon.

Function: Helps keep the melon under tension and makes a strong connection between it and the rostrum.

Delphinus

As in *Tursiops.*

Stenella

As in *Tursiops.*

Major Intrinsic Muscle of the Tubular Sac

Tursiops (Figs. 15, 16)

This is a poorly developed muscle with a strong mixture of connective tissue, particularly in its anterior part. It merges with and vanishes in the adjacent tissue to such a degree that it is extremely difficult to determine its limits. Anteriorly it is thick, with the muscle fibers becoming sparser as one dissects deeper. The direction of the fibers is difficult to determine; posteriorly they run anteromedially and gradually change direction to run posteromedially in their anterior part.

Origin: In the fatty, collagenous connective tissue between the tubular sac and the skull posteriorly and laterally. It also attaches in a thick mass of this same tissue on top of the connecting sac. Anteriorly it intermingles with the connective tissue insertion of *ai.*

Insertion: On the margin and underside of the tubular sac, the anterior part being attached more on the underside and less on the margin.

Function: The posterior part helps to anchor and hold open the tubular sac; the part lying between the tubular and connecting sacs may also help to separate the walls of the latter.

Delphinus

The structure of this muscle was exceedingly hard to determine here. The anterior part in particular was not clearly separable from the surrounding layers.

Stenella

As in *Delphinus*, this muscle seems to be largely posterior. It differs from that in *Tursiops* in having the fibers run anteromedially to insert on the tubular sac. Thus while the anchoring effect is apparently the same, the direction of the fibers is different. It should be emphasized again that this muscle is poorly developed and hard to trace.

Ligament Muscle (not figured)

Tursiops

This poorly developed band of muscle fibers is apparently an internal slip of the major intrinsic muscle, with which it is closely connected. It lies beneath and in front of the blowhole ligament, on top of the connecting sac.

Origin: Beneath the blowhole ligament.

Insertion: In the tissue near the commissure of the slitlike opening above the plugs.

Comments: Failure to identify this slip in *Stenella* and *Delphinus* could easily have been due to the great difficulty of separating it from the rather formless mass of connective tissue and muscle fibers in this area. A special effort to determine its extent in *Lagenorhynchus* showed it to be distinguishable from the major intrinsic muscle only by the direction of the fibers. In *Lagenorhynchus* the ligament muscle, as well as inserting near the commissure, has a few fibers that insert in the outer wall of the premaxillary sac where this latter overlaps or lies on top of the lip of the plug. It is possible that this helps open the passage here.

Minor Intrinsic Muscle of the Tubular Sac

Tursiops (Fig. 15)

A very poorly developed muscle wrapping around the anterior part of the posterior half of the tubular sac.

Origin: In the fatty collagenous connective tissue between the tubular sac and the nasal passage both internal and anterior to the tubular sac, so that the fibers trend dorsoposteriorly.

Insertion: Weakly around the anterior part of the posterior half of the tubular sac.

Function: As with the major intrinsic muscle of the tubular sac, this helps to anchor and hold open the tubular sac.

Delphinus

Not found here, possibly due to state of preservation.

Stenella

Relatively better developed here than in *Tursiops,* and passing across the tubular sac near the bend to merge with the major intrinsic muscle of the tubular sac.

THE BLOWHOLE MECHANISM

Structure must be understood in order to understand function, but the detailed dissections described above do not by themselves suffice to explain the blowhole mechanism of porpoises. The additional information obtained from experiments on living and freshly killed animals has solved a number of controversial problems which have baffled zoologists in the past.

Observations on its Functioning

All of the evidence agrees in showing that the passage is opened by muscle action, closed by the natural elasticity of the tissues, and the seal is tightened not by muscle action but by forcing the air back up the passage into the tubular sac. Inflation of this sac makes a very efficient seal where the passage narrows to a slit beneath the vestibular sac —— so efficient that internal to this the porpoise can keep its bubble, or internal air, at greater than ambient pressure. It makes a less efficient seal at the blowhole entrance, where it is possible with small effort to separate the lips. When the passage opens, the plugs, the anterior fold of the vestibular sac, and the valve move so nearly simultaneously that pictures at 64 frames per second fail to show any differential sequence of events (Fig. 26), and we could not detect any perceptible lag between the first movement and the outward rush of air. When the passage closes it is possible, again in slow motion pictures, to see the plugs falling into place first, next the anterior fold of the vestibular sac, and finally the valve (Figs. 27, 28).

This opening of the passage is in no sense the separating of the lips of an orifice; it is the drawing apart of masses of tissue which, when undisturbed, lie pressed closely together. Most of the motion is in the anterior part of the passage, the great wedge of tissue formed by the valve, the folds of the vestibular sac, and the plugs being drawn down and forward away from their position beneath and against the posterior wall. Although the posterior part moves relatively little, it is possible to see the mid-part of the crescent drawn back to widen the blowhole aperture (Fig. 26) and to feel the wall inside lifted up and back from its position on top of valve and plugs.

Within the vestibular sac and well behind the opening of the main passage, it is possible to feel a very strong contraction of muscle layer *pe* between the outer wall of the vestibular sac and the blubber as the blowhole opens. Deeper than this, individual action of the muscle layers cannot be felt, although it is easy to feel the swift separating of the actual walls of the passage. It is, however, apparent from their arrangement and the relative strength of their parts as well as from pulling on them by hand, that *pe* and *pi* control the posterior wall of the passage, drawing the lip slightly back and lifting the wall of the passage, including the convex mass, away from the valve and dorsal surface of the plugs. Layers *ae* and *ai* act on the anterior mass external to the plugs, drawing the valve and anterior fold of the vestibular sac forward and down. Finally, the nasal plug muscle withdraws the plugs from their position across the bony nares.

The nasal plug muscle attaches in the cushion of the plugs, and of necessity it is that part of each plug which lies against the posterior wall beside the septum which must move the most to open the passage. The liplike, lateral extension of the plugs is moved only indirectly, and very little, as is shown in motion pictures. This shows less clearly in the photographs, but in Figure 26 this part of the plug shows near the back corner of the otherwise widely opened passage. There is also very little motion at the lower end of the plugs where they attach on the cartilaginous septum close to the anterior margin of the bony nares (Fig. 19). For this reason, withdrawing them does not open the premaxillary sac, nor can the plugs slide forward into the sac. Instead, the plugs hinge here and their forward movement makes a distinct and perceptible midline bulge in the melon, which at the same time seems to flatten on the sides. Apart from this bulging of the melon when the blowhole opened, no other muscle action was seen or felt through the thick layer of blubber which covered the *Tursiops* head to a depth of about two-thirds of an inch.

All of this happens very quickly, and during a normal blow the main column of air passes directly and with considerable force to the outside. There is no preliminary inflation of the vestibular sac, as determined by manometer readings, though there is here a very slight rise from 2 mm. of mercury to about

8 mm. during a blow, with readings in the bony nares going up to at least 30 mm. at such times. This rise is part of the general rise in pressure at exhalation, and one sequence of pictures showed a slight bulge over the vestibular sac at this time. On inhalation the pressure drops, and the same sequence then showed a flattening of this area. The pattern of a blow is for the exhalation to take longer than the inhalation. This can best be told by ear, as there is no visible change in the widely opened passage when exhalation stops and inhalation begins. The timing of events during the period between the first opening of the blowhole and its complete closing varies. In eight blows of a single individual loafing near the surface, it was found that the percentage of time for opening the blowhole averaged about the same as that for closing, though sometimes the one was swifter, sometimes the other, and on two occasions the blowhole seemed to widen slightly after it was apparently fully open. These blows were analyzed as follows:

Total blow	*Opening*	*Closing*
.63 secs.	17.5%	12.5%
.77	16.3	20.0
.69	19.0	18.2
.77	14.2	14.3
.75	16.6	14.6
.74	14.9	19.2
.78	14.0	20.0
.47	20.0	16.6

That the opening and closing took so nearly the same time is especially interesting in view of the fact that only in closing is there a clearly visible sequence of events (Figs. 27, 28). At this time the plugs fall in place first, then the folds of the vestibular sac, and last the valve. More often than not the closing appears asymmetrical with, in two porpoises at least, a lag on the left side.

As is often the case with aquatic mammals (Howell 1930, p. 87), the closed position is the involuntary one. In the forms studied this is dependent on the great elasticity of the tissues. The posterior lip presses on top of as well as behind the anterior, so that when it is pulled up by hand and released it falls back quickly in spite of the absence of any muscles to draw it in this

direction. Similarly, the valve when depressed by finger immediately lifts into place when the finger is removed. A finger inside the vestibular sac during repeated blows detected no muscle action between the sac and the blubber to pull the lips of the blowhole together, nor does anatomical investigation show any muscle capable of this action. Air is not retained in the vestibular sac at the end of a blow, as repeated investigation of the live animal showed. Manometer readings showed no pressure here at such times, and opening only the vestibular sac by separating the lips of the blowhole right after an inhalation never resulted in the escape of air, even when this was done under water. Beneath the vestibular sac, the passage narrows, as previously described, to a transverse slit between the top of the plugs and the posterior wall of the passage. The soft mass of the anterior fold of the vestibular sac covers this slit so completely that considerable probing is needed to get into the passage beneath it. In the posterior wall internal to this slit, the elastic blowhole ligament and associated tissues form a taut convex mass which is difficult for the finger to lift from the top of the plug, and which immediately snaps back into place when released. Deeper than this it is possible further to open the passage by unseating the plugs manually. This does not necessarily result in the escape of air, indicating that at such times, anyhow, the animal's internal air is at no greater pressure than his surroundings.

Attempts to open forcibly different parts of the nasal passage showed that when the *Tursiops* resisted it did so by inflating the tubular sac. This resistance could be felt strongly internal to the vestibular sac and weakly at the lips of the blowhole. Within the vestibular sac over the posterior part of the tubular sac, an obvious swelling could be felt at such times, and when a finger was forced down the slit between the plugs and the posterior wall a tightening could be felt on each side of the finger. Further, when the porpoise was thus resisting, manometer readings in the lateral margin of the premaxillary sac showed sharp rises in pressure, measured in millimeters of mercury above ambient (= 0 mm.). At these times the pressure fluctuated irregularly, the usual pattern being for the animal to hold pressures of about 6-10 mm. and sometimes as high as 20 mm. between blows, with

occasional rapid excursions higher. The greatest pressure recorded at such a time was 124 mm., though peaks were more often between 40 and 60. On the inhalation the pressure dropped to about 0. Also at times of resistance there was often a slight but appreciable bulging of the melon somewhat in front of the valve, as might be caused by inflation of the premaxillary sac. With the manometer tube at the entrance to the tubular sac, similar changes in pressure were recorded. These were somewhat more erratic, probably because of leaks around the rubber tube, and reached as high as 86 mm.; as with the premaxillary sac, the pressure dropped at the end of each blow, seemingly on the inhalation. Clearly, efforts to hold the blowhole closed involved forcing air back up the passage under considerable pressure; unless the plugs were unseated by hand, or the walls of the passage near the entrance to the connecting sac were separated, this air did not escape but was retained internal to the vestibular sac.

More often than not the porpoise made no perceptible resistance to our explorations of the vestibular sac, as he almost always did when we tried to push further down the passage. On the not very frequent occasions when the porpoise resisted separating the lips of the blowhole, a lifting of the cushion of the valve as by inflation of the tissue beneath it could be felt, sometimes accompanied by what seemed to be an inflation of the premaxillary sac. The lifting was immediately external to the anterior part of the tubular sac and made a visible depression along the hinge line of the valve. This, however, was not strong enough to prevent the valve from being forced down by hand with very little effort. When this was done with the blowhole submerged, water ran into the vestibular sac. At the next blow, the water was ejected.

That this use of the vestibular sac as a water trap is not accidental was suggested by many pictures of swimming porpoises in which one frame shows the blowhole well open with the water at the margin, and the next frame shows the blowhole submerged. This evidence was later confirmed by a long series of similar observations of another porpoise floating at the surface in a confined space. Here sequence after sequence showed the animal submerging with the blowhole open (Fig. 29). As it went under, the water trickled in at the forward corner of the blowhole, on either side; if it delayed closing for .05 to .06 second, the trickle

spread to a stream extending around the rim of the opening to the midline in back. At such times there was often a visible spurt of air and water as the animal submerged while closing the blowhole (Fig. 29), suggesting that if there is any danger of the animal flooding itself, it forces air back up the passage at the end of an inhalation. The spray was particularly conspicuous if water had been allowed to trickle in along the midline, that is to say, posteromedial to the entrance to the vestibular sac. Water leaking in here could not be trapped in this sac, and the only way to get rid of it would be to blow it out. Only part of the water was ejected in this way. On the subsequent blow, a thick spray was apparent before pictures showed a visible opening of the passage (Fig. 30). When the spray was fairly well dissipated the blowhole began to open visibly; in seven sequences this delay varied from .05 to .12 second, depending apparently on the amount of water blown out. This seems to indicate that the animal may force air up the passage, as explained below, without retracting the plugs, while there is water in the vestibule. This would eliminate the danger of water making its way down into the bony nares past the plugs when the animal pulls them. If this should happen it could endanger the larynx or the Eustachian tube, as the porpoise has no mechanism for getting rid of water once it is in the inner nares. The larynx projects into the back of the bony nares and is held in place by a sphincter muscle in such a way that a shallow trough is left around the two, near the bottom of which is the opening of the Eustachian tube. We do not see how water accumulating here, ventral to the opening at the end of the larynx, could either be blown out or ejected by muscle action.

The mechanism for closing the blowhole is not strong enough to retain any volume of air in the vestibular sac under much greater than ambient pressure. Small quantities of air can, however, be trapped in this sac beneath the folds. This was demonstrated in two ways. A small amount of latex blown into the vestibular sac from the inner passage will fill the space beneath the folds, but not reach the outer part. Experiments in pumping air up the nasal passage of a *Delphinus* soon after death show that after the tubular sac has been inflated, slightly more pressure will inflate the vestibular sac with scarcely any air escaping from the blowhole. Apparently, under moderate pressure, air from

below will lift the anterior fold up against the posterior lip, thus tightening the seal, which helps to trap air in the inner part of the vestibular sac. When internal pressure is released, the sac deflates slowly, and it is difficult to force out the residual air by hand pressure. Similarly in a dead *Lagenorhynchus* where air was found in the tubular sac, this air could be forced into the vestibular sac when the anterior part of the tubular sac was squeezed by pulling *ai*. When this tension was relaxed the air moved back into the tubular sac. It did not escape at the blowhole nor did it find its way past the plugs and out at the cut end of the trachea.

These two experiments seem to show that once the tubular sac is inflated, as in the first case, it is difficult to force air past the slitlike opening which it constricts. If, on the other hand, the tubular sac is squeezed more or less empty, as in the second experiment, air passes more easily through this slit in either direction. The fact that air returned to the tubular sac when pressure was released would seem to indicate that this sac ordinarily remains partly open. Anatomically, particularly at the bend, this is possible. Of further interest is the presence of observable amounts of air in the outer passage of this individual only, among the various ones dissected. Since the animal was harpooned and lanced, and died after considerable flurry, it seems very likely that this tightening of the seal of its air passage was part of its death struggle.

Anatomical Explanation of Function

The observations on the various changes that take place in the outer nasal passage during and between blows are both confirmed and explained by the accumulated anatomical data. The absence of muscles for closing the blowhole was striking. No muscles were found on top of the vestibular sac with attachments near the corner of the crescent which could possibly draw the posterior lip forward. Instead, the two large layers, *pe* and *pi*, attaching posterior to the passage, have medial attachments and exert a strong posterior pull. Similarly the wide spread of the vestibular sac and the position of the plugs make it impossible for muscle action to lift the valve up and back against the posterior lip. The two layers, *ae* and *ai*, which attach in front of the

passage beneath the valve, pull strongly downwards and forwards. In each instance the outermost layers attach well beneath the thick layer of blubber and connective tissue which surrounds the orifice, far too deep to draw the edges together in any way.

While elasticity of the tissues closes the passage, the normal watertight fitting together of its parts is ensured by the texture of the surfaces and consistency of the masses involved. In the posterior wall there are two stiffened and very smooth surfaces. The more external is the underside of the crescentic posterior lip, which closes against the equally smooth anterior wall where it slopes posteroventrally from the valve. The more internal is the convexity formed by the posterior part of the tubular sac and the associated muscles and connective tissue, and stiffened by the blowhole ligament. This, too, has a very smooth surface which lies in the no less smooth concavity of the external surface of the plugs. Between these two stiffened surfaces is the soft wrinkled mass of the two folds of the vestibular sac. Thus between two pairs of beautifully conforming surfaces there is a gasket-like cushion that can be distorted to fill any crack.

The pneumatic closing action of the tubular sac is also easily understood if the structure of this region is examined in detail. As is most readily seen in sagittal section, the plugs lie diagonally across the upper end of the bony nares in such a way that air under pressure from below will push the posteromedial part of the plugs more tightly against the surface dorsal to them, thus hindering the direct upward passage of air while at the same time lifting the lateroventral part of the plugs to open the entrance to the premaxillary sac so that air can pass in this direction. While the cushion of the plug is thus lifted by air forced up the bony nares, the lateral extension is not so affected, lying as it does on top of the protecting diagonal membrane and the premaxillary bone. This means that this part of the plug is not pushed up against the entrance to the tubular sac, which thus remains open while the main passage closes more tightly. From the premaxillary sac air passes into the connecting sac, whose opening lies immediately above the lateral external opening of the premaxillary sac. From here the direct upward passage of air takes it into the tubular sac, whose intrinsic muscles are suited to open it, facilitating the passage of air in this direction. As described above, this inflation of the tubular sac tightens the

seal of the passage. When latex was blown up the passage of a *Delphinus*, a concentration of it was found in the lateral edge of the premaxillary sac continuous with the latex in the bony nares and that lying external to the lip of the plug. This shows how air from the premaxillary sac thus passes externally to the plugs into the connecting sac.

There is no evidence that hydrostatic pressure is important in sealing the blowhole. Animal tissue differs little from water in its compressibility; so, once the outer passages are emptied of air, sea pressure could be used in this way only if the air in the bony nares were at less than ambient pressure, and the porpoise's voluntary efforts to tighten closure of the passage involve, as we have seen (pp. 133-134), a rise to greater than ambient. This is surely the easiest arrangement, for achieving an intrapulmonary pressure less than ambient would involve expanding the thorax, which would be difficult at any but the shallowest submergence. To put it differently, this postulates the animal working against its medium (the water) to tighten the closure of its nasal passage when it is organized to do this much more easily by working with the medium. It is further significant that in relying on an increase in internal pressure to tighten its seal, the porpoise has perfected an arrangement which allows it to retain its internal air under greater than ambient pressure.

Contrast with Mysticetes

The reasons for these complications in the porpoise's outer nasal passage are not completely understood. Aquatic mammals in general develop some mechanism for closing the nostrils. In delphinids this is particularly elaborate, far more so, for instance, than in their relatives the baleen whales. Both groups are faced with many of the same problems, and the different ways in which they have solved these must inevitably depend on the variation possible in each group. In the mysticetes, or baleen whales, the nasal passage is much less modified than in the odontocetes. The nostrils are still paired, the passage is more nearly horizontal, and partly roofed over by the nasal bones. All this has made possible a comparatively simple method of closing. In one form dissected, *Balaenoptera acuto-rostrata*, which is probably fundamentally similar to the others, the nares are closed

by two large plugs moving on each side of a stiff median septum. These pass beneath the posterior wall which is stiffened by cartilage. Posterolateral to this opening of the inner passage and extending anteriorly are shallow diverticula which probably form the basis for Kernan's somewhat misleading and oft-quoted reference to "spiral folds" as a closing device (Kernan *in* Schulte, 1916, p. 435). The muscles opening the nostrils and moving the plugs are simple, and the elasticity of the tissue as felt when one thrusts an arm down the nasal passage of a dead whale is surely great enough to close it. There has been no development of an elaborate pneumatic mechanism to tighten closure.

Both groups of cetaceans have in common their need for some way to keep water out of the inner passage. Stormy weather and fast swimming with a minimum of time at the surface make this a real problem for each, but the solution is different. The odontocetes, as we have discovered, have a water trap inside the blowhole. The mysticetes have a conspicuous V-shaped pair of ridges which elevate in front of the nostrils as these open. Observations at sea of the humpback, *Megaptera novae-angliae*, and the little piked whale, *Balaenoptera acuto-rostrata*, show these to be very efficient water deflectors, at least in moderate weather.

The use of buoyancy changes may also be common to both groups, although we have not observed it in the mysticetes. We have frequently seen our captive *Tursiops* sink vertically. This sudden sinking without exhaling and without any horizontal motion (thus excluding the possibility of planing forces driving the porpoise down) seems best explained by a buoyancy reduction from making the body smaller. This could be done only by compressing the internal air, which requires a tight seal in the respiratory passage; since human swimmers can do this in slight degree, it is not surprising to find a cetacean adept at it. Such a maneuver differs from the sinking after exhaling often observed by us in *Stenella plagiodon* and reported by Woodcock and McBride (1951, p. 215). One is reminded of the old whalers' accounts of "settling" by the sperm whale, supposedly as an emergency maneuver when surprised by a whale boat (e.g., Davis, 1874, p. 187).

Different solutions to similar problems based on fundamental

dissimilarities in structure only partly explain the elaborate pneumatic arrangement of the odontocete passage. Other differences based on different habits and activities must also contribute. One of the most conspicuous features of the odontocetes, and one in which they differ widely from the mysticetes, is their habitual production of a wide variety of underwater sounds. Experiments have led us to believe that these sounds are laryngeal, and we have found that they all can be made without necessarily allowing air to escape from the blowhole. Undoubtedly the ability to subject the internal air to considerably greater than ambient pressure is important in this connection. Regulation of the air pressure in the sinuses connected with the middle ear may also be affected by this arrangement, much as a noseclip aids a human diver, especially if he goes deep.

DISCUSSION OF PREVIOUS WORK

Much of the early work on the blowhole region does not deal with function, and since this is our main interest an historical account of these investigations is not attempted here. The reader who wishes to pursue this can find fairly detailed references in Murie (1873) and Gruhl (1911). It is, however, opportune to summarize the varying opinions on the manner in which the outer nasal passage is opened and closed and the anatomical evidence on which these opinions rest.

Since the early 19th century there have been two general theories; the one held by such workers as von Baer, Kükenthal, Boenninghaus, and Gruhl, that the blowhole closes when its muscles relax and is sealed tighter by increasing hydrostatic pressure, and the other held by Cuvier, Sibson, Murie, and more recently by Huber and others, that certain of the layers of blowhole muscle pull the blowhole closed while others open it. Further, there are differences of opinion as to the number of layers involved. The first group of workers tends to emphasize the essential singleness of the blowhole muscle in structure as well as in function. The second group, in accordance with the double function they assign to this musculature, defines numerous layers. Thus, those workers who believed the blowhole to be opened, not closed, by muscle action felt it unnecessary to recognize more than a very few layers, while those whose approach is

through dissections (accurately showing more numerous muscle layers) have felt it necessary to assign a double function to these. Neither group has adequately described or shown the use of the nasal sacs.

A considerable part of these investigations was carried out on *Phocoena*. Piecing together the accounts of phocoenids by von Baer, Kükenthal, Sibson, Boenninghaus, Gruhl, and Howell, one finds a certain similarity in structure between these and the delphinids, but the differences are such that more anatomical detail and an actual examination of live specimens is necessary before function can be compared in the two groups. However, we see no reason to doubt von Baer's assertion of 1826 (col. 820) that the lips of the blowhole are closed except when opened by muscles. Turning to the delphinids, we find that the earliest good descriptions and illustrations of the blowhole region and associated muscles in this group are those of Murie, who published on *Grampus rissoanus* (= *griseus*) (1870), *Lagenorhynchus albirostris* (1871), and *Globicephalus melas* (= *Globicephala melaena*) (1873), stating in the latter paper (p. 247) that the function of the layers is "nearly identical in the several forms." Of these genera the second is the most closely related to the three discussed in this paper, and dissection by us of *Lagenorhynchus acutus* shows this species, at least, to resemble our three closely. In this it disagrees with Murie's figures of *L. albirostris*, which differ chiefly in the wide areas of insertion of the outer layers of blowhole muscle, structure and musculature of the tubular sac, and the arrangement of the rostral muscles. In spite of this, a comparison of his text and figures leads us to believe that his layers (1871, pp. 147-148 and pl. 5) may be homologized with ours as follows: first layer, occipito-frontalis, with *pe*, and probably also *i;* second layer, levator labii superioris alaeque nasi, with *ae* (the posterior part is probably homologous with our inner layer of *pe* which we found merging with *ae*); third layer, levator superioris proprius, with *pi;* fourth layer, zygomaticus, and the posterior part of the fifth layer, depressor alae nasi, jointly with *ae* and *pr;* the anterior part of the fifth layer, which he calls naso-labialis, with the pars labialis of the maxillonasolabialis. The nasal plug muscle is described (1871, p. 149) but not named or figured. Finally pyramidalis, in spite of its difference in size and orientation, is probably equivalent to our

major intrinsic muscle of the tubular sac. Murie's sacs also may be homologized as follows: the maxillary with our vestibular sac, the naso-frontal with the posterior part of our tubular sac, and the anterior or premaxillary with our premaxillary sac. While our examination of *Lagenorhynchus* was not as thorough as that of the other three forms, we found nothing to suggest that it functions differently. In spite of this strong similarity, we also found that as a group *Tursiops*, *Stenella*, and *Delphinus* resemble each other more closely than any of them does *Lagenorhynchus*. In some features this latter, a shorter beaked porpoise, tends to approach *Globicephala*. Although the evidence is not conclusive, the resemblance (in such detail as Murie published) of *Grampus* and *Globicephala* to our material suggests very persuasively that here also function will be found to be very similar. Our own superficial examination of the passage and sacs in *Globicephala* tends to confirm this. Murie himself felt this to be true of his forms and so stated (see below) in the last of his three accounts. His work on *Globicephala*, although completed first, was not published till after the other papers had come out. His work on *Grampus* was completed next and published first, while that on *Lagenorhynchus* refers to both of the previous dissections. Homologous outer layers are given the same names in all three although they are sometimes numbered differently. Identification of the inner layers varies, and one more layer is recognized in *Lagenorhynchus* than in the other two. This inconsistency is based not so much on an apparent difference in the layers as on attempts to homologize them with facial muscles of other mammals, and so does not concern us here. What is of interest is Murie's inability to come to any single, final conclusion as to the functions of these layers in spite of his statement (1873, p. 247): "As regards the action of the different layers in *Globiceps* etc., they are nearly identical in the several forms." In the paper on *Grampus* he says that the three outer layers close the blowhole while the fourth layer opens it, as does also the nasolabialis. In the paper on *Lagenorhynchus* he claims the opposite function for these same three, saying they "dilate" the blowhole; the use of the fourth is more obscure: he appears to feel that primarily it helps close the passage by compressing the nasal blubber, while it could also have a tendency to open the blowhole; the fifth layer he feels has a divided function: the anterior part (1871, p.

149) "drags forward and everts the anterior lip," the posterior part retracts it. Evidently in *Globicephala* the various layers function as in *Lagenorhynchus*. This is apparent when on comparing text and figures (1873, pp. 247-248, figs. 63-65), it becomes clear that the "superior layer" of *Globicephala* equals occipito-frontalis and levator labii superioris alaeque nasi (the first and second layers of *Lagenorhynchus*), while the "second sheet" equals levator superioris proprius (or the "third layer" of *Lagenorhynchus*). Clearly, he frequently had in mind that what applied to the blowhole mechanism of one genus was equally true of another, as witness his numerous cross references in lieu of restatement. Nevertheless, he never summarized or clarified these conflicting remarks, and his sequence of dissections and publication is such that it is not possible to decide what his final conclusions were. Although this might make his work seem confused, one has only to consider how difficult his dissections must have been to realize how remarkable it is that he was able to find out so much. As regards the anterior part of the nasolabialis, he seems to understand that this has an opening function, though, as in the case of the other layers, the actual region of the nasal passage affected is not made clear.

Kükenthal's (1893) discussion of the odontocete nose in his monumental whale monograph is chiefly concerned with homologies and phylogeny. He adds little to what von Baer had long before said of function, and his anatomical work bearing on these matters is adequately built on by Gruhl (1911). Gruhl's important comparative account of the nasal passage in the Cetacea deals primarily with odontocetes, of which he dissected four genera, and includes a detailed discussion of previous work. His comments on function and such anatomical details as he gives for *Tursiops* and *Delphinus* need to be considered here. Very properly he realizes that elasticity of the walls closes the passage, but he dismisses the musculature as essentially a large paired muscle which embraces the outer sacs and is suited to widen them. As with previous workers who have understood the basic single function of the blowhole muscle layers, there is no apparent grasping of the fact that the valve moves in one way, the posterior wall of the blowhole in another, and the folds of the vestibular sac still differently. It is this difference in the way particular parts of the nasal passage have to move in order for

it to open which has made it necessary for the musculature to be organized in alternating layers with differently directed fibers attaching in specific places, not all around the blowhole. In describing the sacs in *Tursiops* and *Delphinus* he calls attention to considerable variation in them, particularly in the connecting sac, which he found to be smaller in *Delphinus* than in *Tursiops*. This is in agreement with our findings. However, his lack of live or fresh material has led him to believe that the small size of the tubular sac means that it is a mere vestige of the "Regio olfactoria," and hence insignificant. He also thinks that the function of the premaxillary sacs is to facilitate the action of what we call the nasal plugs. His detailed and careful description of what we have called the blowhole ligament is of particular interest in that he refers to it as a cartilage. This suggests that chondrification may be more usual than we found it.

Apparently disregarding Gruhl's work, Kellogg (1928, pp. 194-195; 1938, pp. 659) refers to a muscular closing of the nose which he describes (1928) as follows: ". . . the narial cavity is divided into a series of pockets into which the narial passages open, and between these pockets are a series of plugs controlled by muscles that apparently contract when pressure is exerted on the external flap of fibro-elastic cartilage that covers the external nostril." There are no further anatomical details nor explanations, and since this description does not agree with what we have seen, we are at a loss to reconcile it with our findings.

The most recent investigations of the blowhole mechanism in odontocetes are those begun by Ernst Huber as part of his careful series of papers on the evolution of the facial musculature of vertebrates. Through studying the innervation in both *Tursiops* and *Monodon* he came to the conclusion that only one muscle, the maxillonasolabialis, is involved. The blowhole layers and nasal plug muscle are derived from the pars nasalis of this muscle and the rostral muscles from the pars labialis. In addition to studying homologies, he also considers the mechanism of the blowhole, returning to the earlier theory that muscle action helps to close it. A posthumously published paper, assembled from his notes and sketches, is very explicit as to how this might be done.

Unfortunately he himself never lived to complete this work, so the anatomical basis for this theory is not sufficiently detailed:

indeed the published schematic diagrams of muscle action do not agree with the figures of dissections. The latter show in more detail than had previously been done the layering of the blowhole muscle, how the outermost layers are more posterior, the inner ones more anterior, and the increasing horizontality of the deeper layers. The direction of the fibers of the pars labialis of the maxillonasolabialis and their continuity with the inner layers of the blowhole muscle are also clearly shown. What are lacking are complete descriptions of the individual layers and their subsidiary parts, their relative thickness, fiber direction, and the minutiae of their insertion, as well as detailed descriptions of the sacs and their relation to the main passage. Probably it is in part lack of this evidence which has led him to conclusions so at variance with what our studies have demonstrated. The assumption that the outer layers of muscle close the blowhole is based largely on their attachment in the tissue on each side of the passage. This is easily seen, and it is interesting to note that while Huber interprets this to mean that they pull the blowhole closed, earlier workers interpreted this as evidence of a dilating action. Actually, if thickness of the layers and insertion of their strongest parts are known, it is perfectly clear that the layers which attach around the passage in this way have a powerful portion which moves one part of the passage so as to open it, and a weaker, thin portion which helps anchor an opposite part against distortion. The deeper layers he believed assisted in closing the blowhole by pulling the "elastic cushion" beneath the valve backward, thus squeezing the valve back and up against the posterior lip. We found no layers which could do this. Either they attach posterior to the passage or too deep for their contraction to have this effect.

Though he thus postulates a closing action for layers which we find open the passage, he also refers (1934, p. 124) to "the dilator musculature of the blowhole orifice." This is not further described or figured so it is difficult to know what muscles or layers he had in mind.

As well as postulating muscle action to close the blowhole, Huber also said that air trapped in the vestibular sac helps to keep the plugs seated; but after a blow we always found this sac empty of air. The pneumatic action which he felt around the outside of the blowhole was probably deeper than he suspected.

His forcing the animal to breathe by pressing here might have been due, as he suggests, to unseating the plugs. We ourselves were only once able to make a porpoise breathe by squeezing lateral to the blowhole, though we tried repeatedly. Unseating the plugs by means of a finger inserted down the passage often made it blow. Sometimes, also, when it was resisting our opening the blowhole it was possible to make it blow by pressing down on the valve.

In respect of these remarks about cetaceans, it is interesting to note that of seals Howell (1930, p. 88) says that two muscles control the nose: the maxillonasolabialis opens it and the nasolabialis closes it. Now we find in cetaceans, where the closing is not by muscle action, that the nasolabialis is rudimentary.

Huber's paper was prepared for publication by A. B. Howell, who gives no indication of disagreeing with the theories therein. However, in an earlier work while speculating on the origins of the sacs, he says (1930, pp. 98-99), "The intricate and laminated muscle layers which converge to operate its opening cannot function as dilators with precisely equal force at each and every point, however, but their pull must be very unequal." This excellent observation is subsequently confused by a statement that the nasal valve (which equals our anterior lip and may also be used here to include the plugs) "is opened by contraction of certain of the rostral muscles, and that in closure there is tension from laterad of the blowhole, but whether [it] is voluntary . . . is not clear." As the rostral muscles, those beneath the melon, are obviously not the same as the intricate muscle layers converging on the blowhole and as he refers the reader to Huber for further details, one gathers that he is in fundamental agreement with the latter. Howell's published diagram (1930, p. 98, fig. 15) is further misleading in that the interlocking arrangements of the supracranial part of the passage are not shown, nor is the attachment of the nasal plug (valvular plug of Huber) to the membranous septum at the margin of the premaxillary sacs. This is what makes it impossible for a forward movement of the plug to open the premaxillary sac as Howell's diagram shows.

"The handbook of R. H. Burne's cetacean dissections" (Fraser 1952), although it does not deal with function, is of interest in that the sagittal sections of *Delphinus* resemble closely ours of *Tursiops*. This is to be expected in view of the close resemblance

we found between the two forms in the arrangement of sacs and muscle layers. Comparing the terms used for the various structures which he found, his "boss" matches well our nasal plugs, while his vestibular and premaxillary sacs are the same as ours. The intermediate areas as shown in his Figure 19 are harder to identify with the structures found in our dissection of *Delphinus*. Apparently the "tongue-like" process equals both our cartilaginous septum and the concave mass of the posterior wall; the "subsidiary sac" seems closest to our connecting sac, while the space above it could easily be the tubular sac. The dissection shown is exceedingly difficult to make without distorting the region, and this probably accounts for the discrepancies between our findings and his.

EFFECT OF HYDROSTATIC PRESSURE ON THE BLOWHOLE MECHANISM

The failure of earlier workers properly to explain the blowhole mechanism has been partly due to lack of observations on living or recently-killed animals. Further, the anatomical basis for these theories has been incomplete. The arrangement of the muscles had been only partly worked out and too little emphasis put on the actual shape of the air spaces. In addition, the relation of pressure to closing the passage had not been properly analyzed. The effect of increasing sea (hydrostatic) pressure on a closed, collapsible container full of air is to reduce the volume of that air so that pressure inside the container is the same as pressure outside. This means that two very common, essentially opposite theories about pressure in relation to closing the passage are false. The first holds that pressure tends to expel air from the animal, thus necessitating a very strong closing mechanism. The second supposes that pressure itself is the closing mechanism — on the assumption that increasing hydrostatic pressure squeezes the lips of the blowhole ever more tightly together.

As far as the first is concerned, the overlapping and close-fitting-together of the lips and walls of the passage form a series of check valves which trap the air so that its relative density cannot make it bubble out. Further, the cetacean diaphragm slopes in such a way as to allow far more compression of the lungs than in land mammals. Thus the porpoise as it submerges

is effectively a compressible closed container of gas, and subject as such to Boyle's law.

The second assumption is equally wrong, since the compressibility of the air bubble results in the animal maintaining an internal pressure equivalent to the hydrostatic pressure around it. If the pressure on both sides of his valves remains the same, any increase in outside pressure squeezing the passage shut would be acted against by an equivalent increase in internal pressure forcing the walls apart. Outside pressure could tighten the seal only if it acted against a lesser inside pressure. This would be possible only if the porpoise could keep its pulmonary air at less than sea pressure, which, as we have said (p. 138), would be a difficult feat involving holding the ribs lifted against very considerable outside pressure. It is far easier for the porpoise to increase than to decrease its internal pressure, and it is just such an increase, as we have shown above, which pneumatically tightens the seal of the passage.

SUMMARY

Investigations have been made on the blowhole and related nasal structures in the delphinid genera *Tursiops, Stenella, Delphinus, Lagenorhynchus*, and *Globicephala*. These have included dissections and pneumatic studies of fresh and frozen carcasses, slow-motion moving pictures, and observations on live animals, both in captivity and at large. We have demonstrated that the nasal passage is opened by muscle action and closed by the elasticity of the tissues, and that this closure may be voluntarily tightened by a pneumatic seal.

The blowhole musculature which opens the passage is incompletely divided into six different layers, of which five are functionally important. Of these, two insert posterior to the passage and three anterior, alternating with each other to do so and overlapping broadly at their origin. Those layers which lift the posterior part of the passage up and back are in general more external and are thickest posterior to the passage; those which draw the anterior part down and forward are more internal and have their main mass anterior and lateral to the passage. The passage is anchored against distortion by thinner portions of these various layers attaching in such a way as to counteract the

pull of each major portion. As the walls of the passage are drawn apart, the plugs covering the opening into the bony nares are withdrawn by an independent muscle. When the passage is closed the posterior wall presses closely on top of and behind the anterior. The outer part of the passage, including the vestibular sac, may be considered as a vestibule. This is used as a water trap when the animal submerges with the blowhole open. Beneath this is a transverse slit which marks the entrance to the deeper part of the passage. Lying around this slit on each side is the U-shaped tubular sac, which can be inflated without withdrawing the plugs and whose inflation tightens the seal at this slit. This control allows the porpoise to keep its internal air at greater than ambient pressure. Beyond a certain limit an increase in pulmonary pressure forces the air past this point and into the vestibular sac, where a small amount can be trapped beneath the anterior fold, any excess escaping at the blowhole, where there are no constricting muscles.

The blowhole mechanism is efficient in protecting the inner passages from flooding and also in allowing the porpoise a certain independence from its medium in controlling its pulmonary pressure. The odontocete nose is so much more complicated than that of the mysticetes that it suggests other non-respiratory functions. Of these, buoyancy reduction, vocalization, and pressure equalization in the sinuses connected with the middle ear are probably all important.

ACKNOWLEDGMENTS

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The drawings were made by Miss Jessie H. Sawyer. Photographs of transverse sections were taken by Mr. Frank S. Essapian, and the motion pictures by the authors.

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EXPLANATION OF FIGURES

All of the figures are of *Tursiops truncatus* (Montagu).

The dissections are of a young female (skull length about 150 mm.), the sagittal sections of an old female, and the transverse sections of an old bull.

In Figures 1, 21-23, and 26-30 the anterior end is at the bottom of the picture; in all others except the transverse sections it is at the right. Orientation of the head is the same in Figures 10, 11, 13-17, and 19.

Abbreviations used:

Layers of the pars nasalis of the maxillonasolabialis muscle

pe, posteroexternus
ae, anteroexternus
i, intermedius
pi, posterointernus
ai, anterointernus
pr, profundus

MAJ. INT., major intrinsic muscle of tubular sac
MIN. INT., minor intrinsic muscle of tubular sac
VEST. S., vestibular sac
TUB. S., tubular sac
CONN. S., connecting sac
PREMAX. S., premaxillary sac

Fig. 1. Plan of nasal sacs in dorsal view, and positions of sagittal sections, Figs. 2-4. In vertical sequence the vestibular sac is the outermost, then the tubular, the connecting, and the premaxillary. The posterior wall of the bony nares is stippled lightly; the margin of the premaxillary sac is shown by a broken line, the posterior margin of the plug by a solid line. The left vestibular sac is omitted.

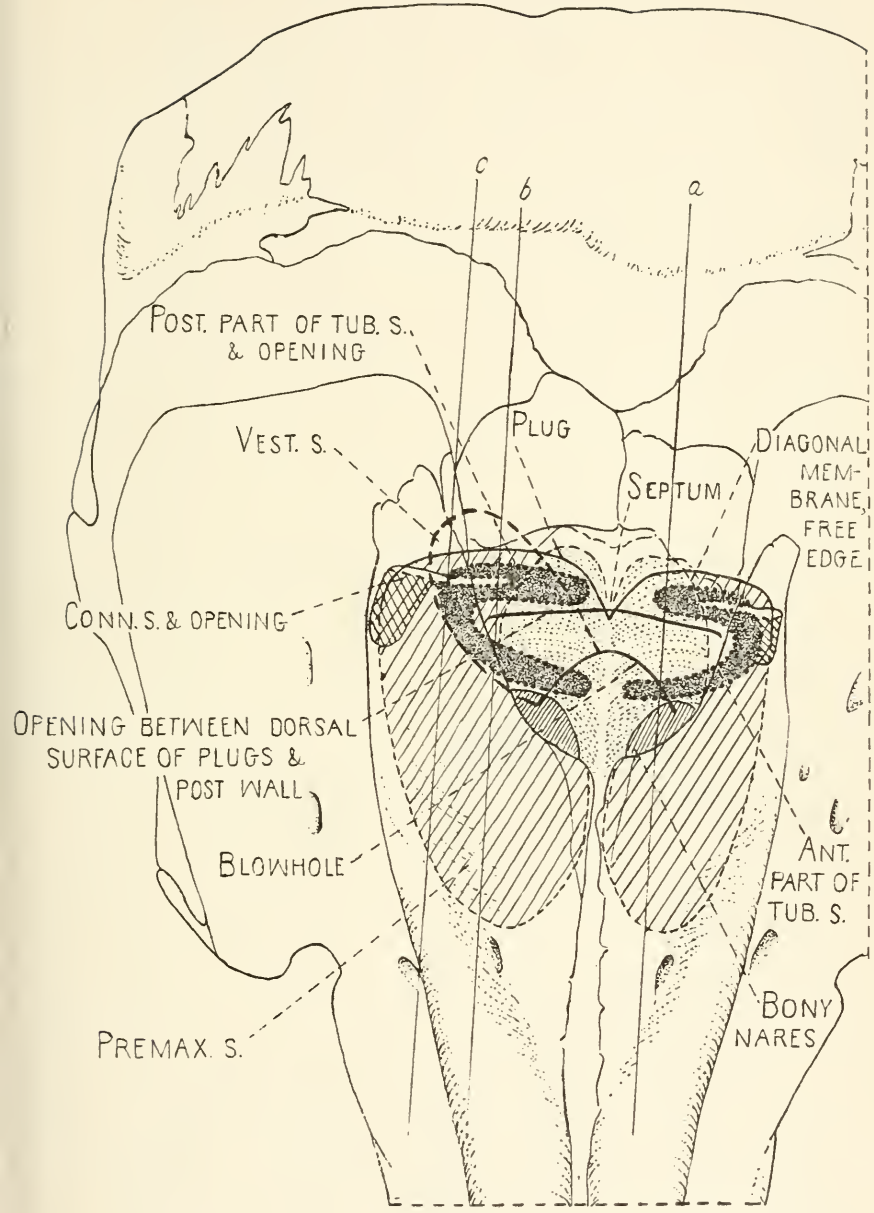

c
b
a
POST. PART OF TUB. S. & OPENING
VEST. S.
PLUG
SEPTUM
DIAGONAL MEMBRANE, FREE EDGE
CONN. S. & OPENING
OPENING BETWEEN DORSAL SURFACE OF PLUGS & POST WALL
BLOWHOLE
ANT. PART OF TUB. S.
BONY NARES
PREMAX. S.

Fig. 2. Sagittal section through blowhole made at *a*, Fig. 1.

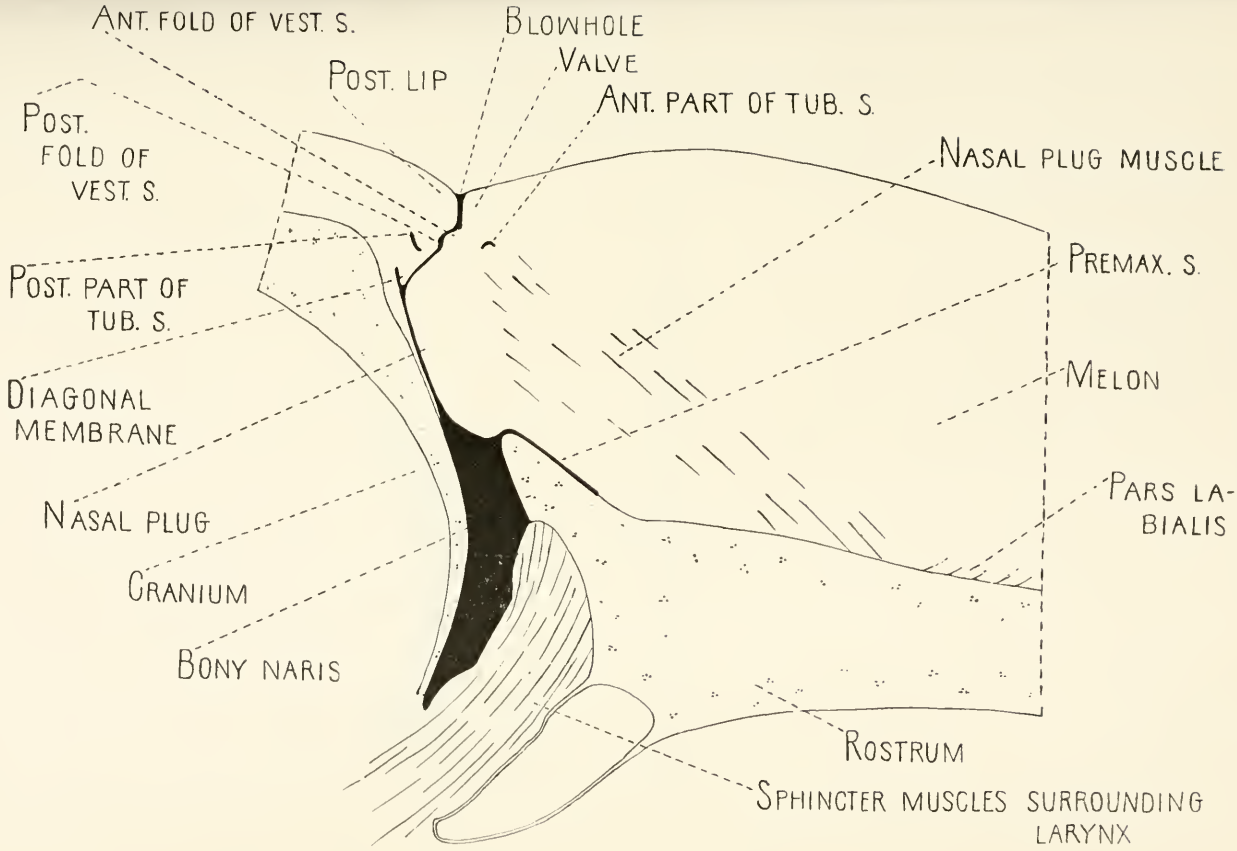

ANT. FOLD OF VEST. S.
BLOWHOLE
VALVE
POST. LIP
ANT. PART OF TUB. S.
POST. FOLD OF VEST. S.
NASAL PLUG MUSCLE
PREMAX. S.
POST. PART OF TUB. S.
MELON
DIAGONAL MEMBRANE
PARS LABIALIS
NASAL PLUG
CRANIUM
BONY NARIS
ROSTRUM
SPHINCTER MUSCLES SURROUNDING LARYNX

Fig. 2

Fig. 3. Sagittal section lateral to blowhole made at *b*, Fig. 1.

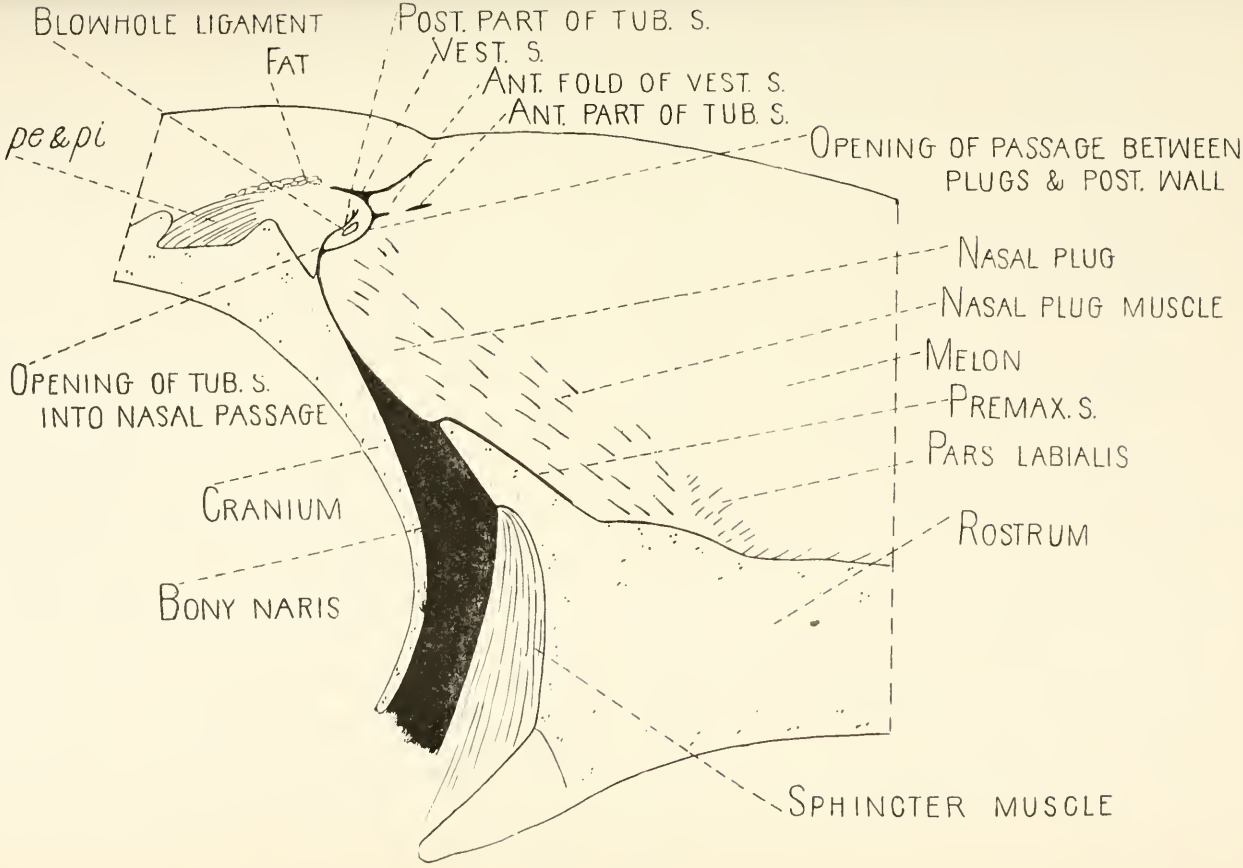

BLOWHOLE LIGAMENT
FAT
POST. PART OF TUB. S.
VEST. S.
ANT. FOLD OF VEST. S.
ANT. PART OF TUB. S.
pe & pi
OPENING OF PASSAGE BETWEEN PLUGS & POST. WALL
NASAL PLUG
NASAL PLUG MUSCLE
MELON
PREMAX. S.
PARS LABIALIS
ROSTRUM
OPENING OF TUB. S. INTO NASAL PASSAGE
CRANIUM
BONY NARIS
SPHINCTER MUSCLE

Fig. 3

Fig. 4. Sagittal section near lateral edge of passage made at *c*, Fig. 1.

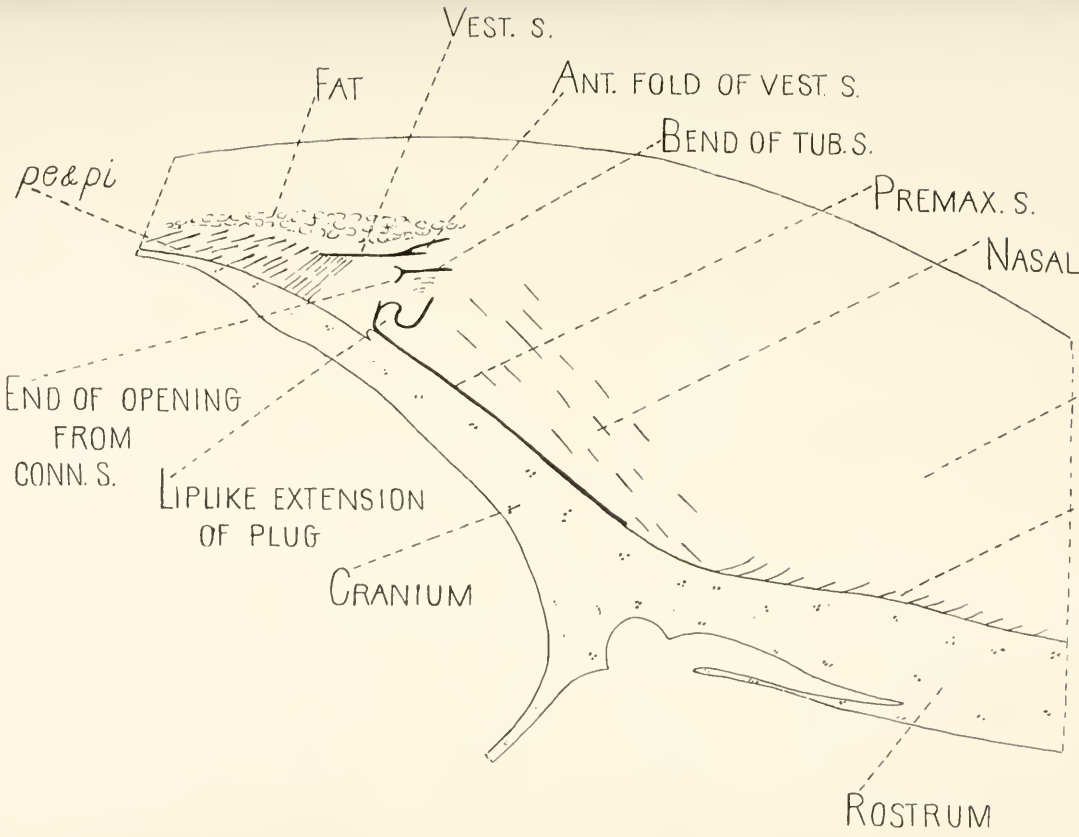

VEST. S.
FAT
ANT. FOLD OF VEST. S.
BEND OF TUB. S.
pe&pi
PREMAX. S.
NASAL PLUG MUSCLE
MELON
END OF OPENING FROM CONN. S.
LIPLIKE EXTENSION OF PLUG
PARS LABIALIS
CRANIUM
ROSTRUM

Fig. 4

Fig. 5. Diagram of sagittal section through right side of nasal passage of fetus with valve and right plug drawn forward to show attachment of cartilaginous septum between plugs. In older animals the larynx lies farther up in the posterior bony nares.

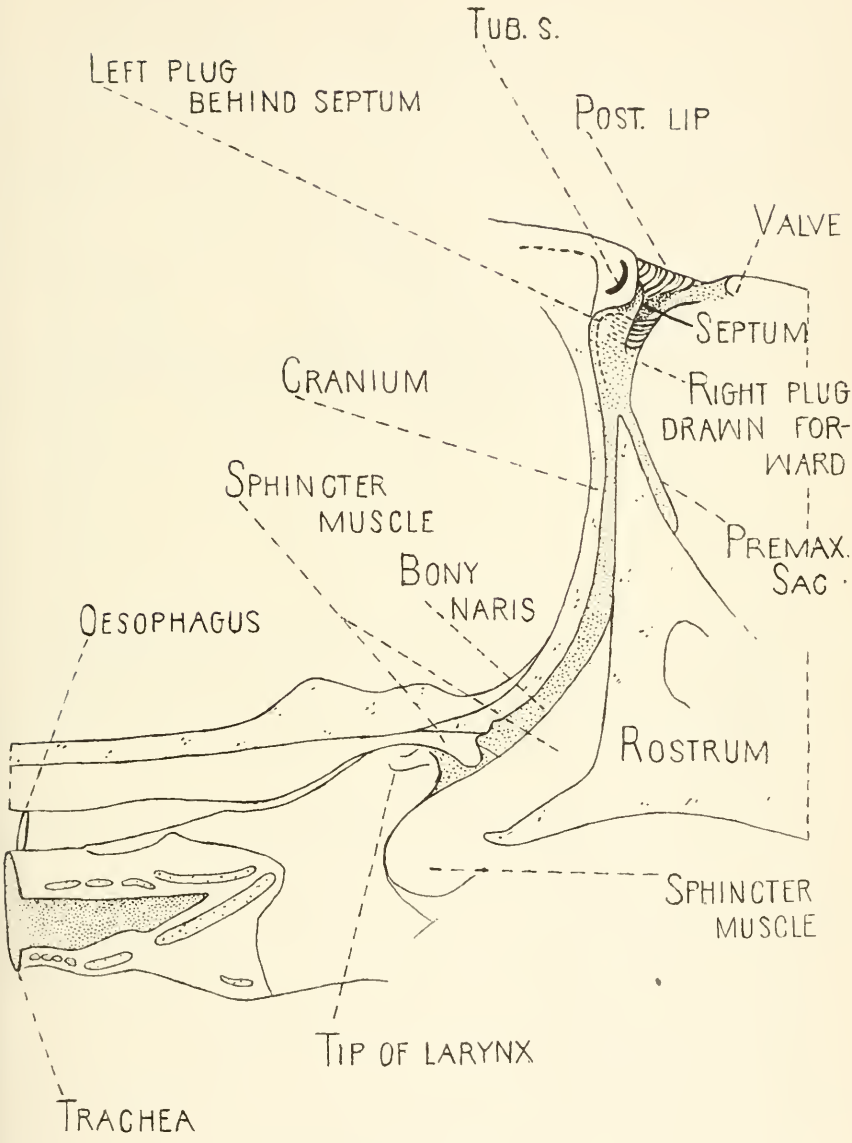

TUB. S.
LEFT PLUG BEHIND SEPTUM
POST. LIP
VALVE
SEPTUM
CRANIUM
RIGHT PLUG DRAWN FORWARD
SPHINCTER MUSCLE
PREMAX. SAC
BONY NARIS
OESOPHAGUS
ROSTRUM
SPHINCTER MUSCLE
TIP OF LARYNX
TRACHEA

Fig. 6. Oblique side view of skull showing positions of transverse sections, Figs. 7-9, 24, 25. The nares are shaded.

Fig. 7. Rostral face of approximately transverse section, posterior to bony nares, made at *a*, Fig. 6, showing relative position of sacs and passage as well as principal separation between layers of blowhole musele. See Fig. 24 for photograph of this same section with passage cut open along lines shown here.

Fig. 6

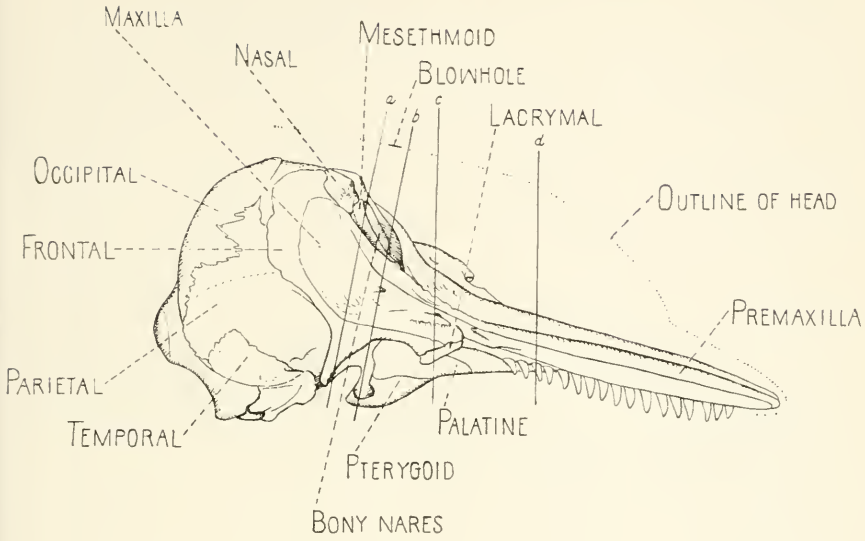

MAXILLA
NASAL
MESETHMOID
BLOWHOLE
LACRYMAL
a
b
c
d
OCCIPITAL
FRONTAL
OUTLINE OF HEAD
PREMAXILLA
PARIETAL
TEMPORAL
PALATINE
PTERYGOID
BONY NARES

Fig. 7

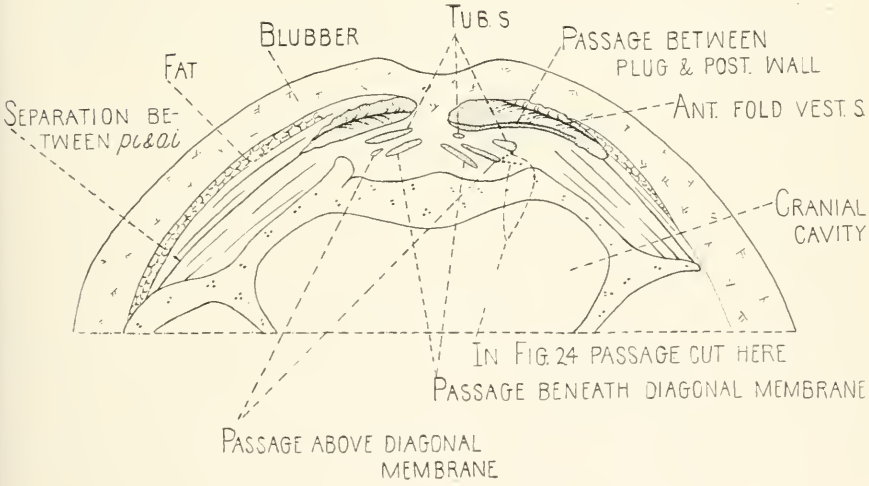

TUBES
BLUBBER
PASSAGE BETWEEN PLUG & POST. WALL
FAT
SEPARATION BETWEEN *pt&ai*
ANT. FOLD VEST. S.
CRANIAL CAVITY
IN FIG. 24 PASSAGE CUT HERE
PASSAGE BENEATH DIAGONAL MEMBRANE
PASSAGE ABOVE DIAGONAL MEMBRANE

Fig. 8. Rostral face of approximately transverse section through bony nares made at *b*, Fig. 6. The heavy black line shows the extent of the paired premaxillary sacs lateral and anterior to the nares. On the left of the figure the lining of the naris has been removed.

Fig. 9. Rostral face of transverse section anterior to bony nares, made at *c*, Fig. 6. The premaxillary sacs are here separated by a thin partition, and the separation between the anterior and posterior layers of the blowhole muscle is well marked.

Fig. 8

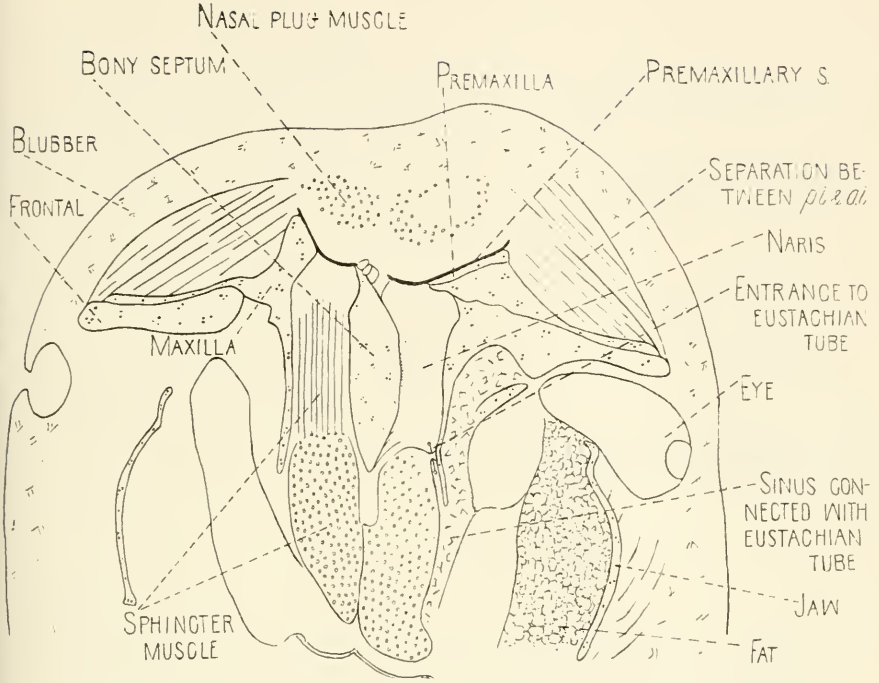

NASAL PLUG MUSCLE
BONY SEPTUM
PREMAXILLA
PREMAXILLARY S.
BLUBBER
FRONTAL
SEPARATION BETWEEN pi & ai
NARIS
ENTRANCE TO EUSTACHIAN TUBE
MAXILLA
EYE
SINUS CONNECTED WITH EUSTACHIAN TUBE
JAW
SPHINCTER MUSCLE
FAT

Fig. 9

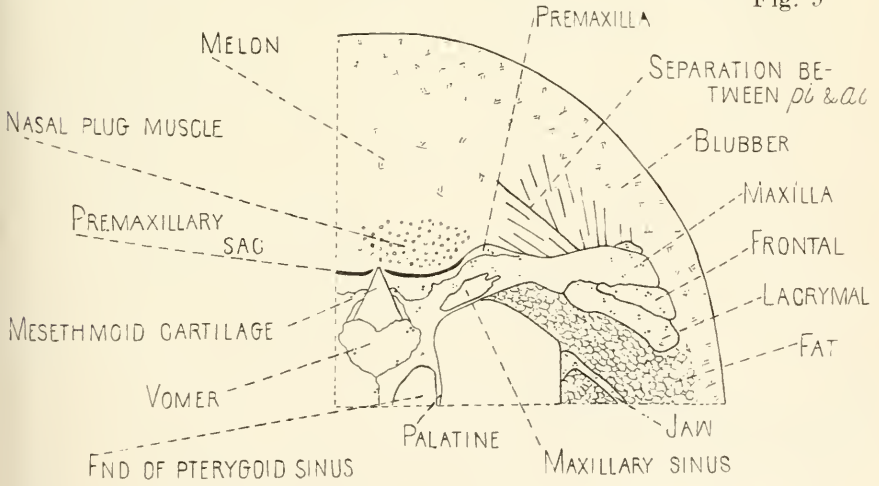

PREMAXILLA
MELON
SEPARATION BETWEEN pi & ai
NASAL PLUG MUSCLE
BLUBBER
MAXILLA
PREMAXILLARY SAC
FRONTAL
LACRYMAL
MESETHMOID CARTILAGE
FAT
VOMER
JAW
PALATINE
END OF PTERYGOID SINUS
MAXILLARY SINUS

Fig. 10. Outermost layers of blowhole muscle; vestibular sac beneath posterior lip dotted in.

Fig. 11. Posteroexternus layer partly cut away to show attachments of outer layers of blowhole muscle on and around vestibular sac, and orientation of deeper layers. The fibrous sheet separating anteroexternus and pars labialis has been reflected.

Fig. 10

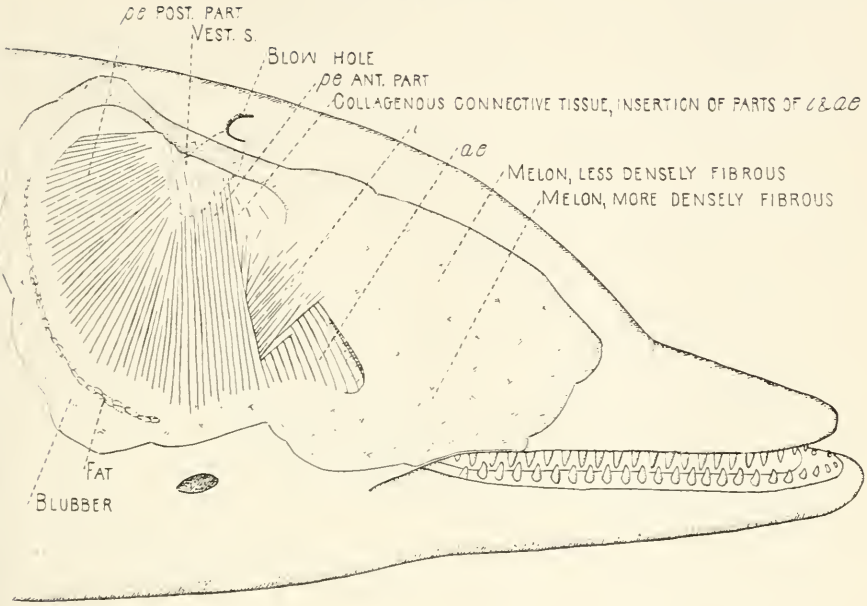

pe POST. PART
VEST. S.
BLOW HOLE
pe ANT. PART
COLLAGENOUS CONNECTIVE TISSUE, INSERTION OF PARTS OF i & ae
ae
MELON, LESS DENSELY FIBROUS
MELON, MORE DENSELY FIBROUS
FAT
BLUBBER

Fig. 11

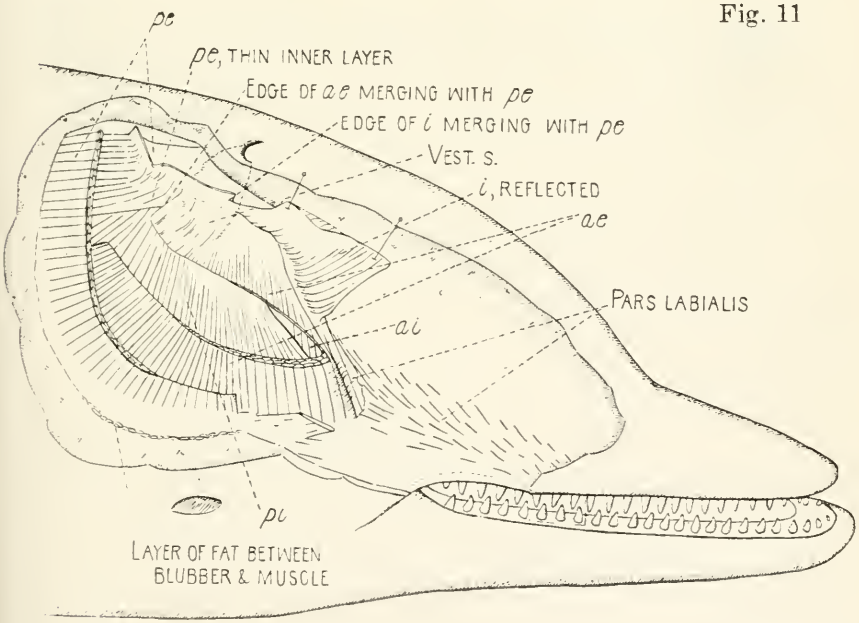

pe
pe, THIN INNER LAYER
EDGE OF ae MERGING WITH pe
EDGE OF i MERGING WITH pe
VEST. S.
i, REFLECTED
ae
PARS LABIALIS
ai
pi
LAYER OF FAT BETWEEN
BLUBBER & MUSCLE

Fig. 12. Dorsal view of outer layers of blowhole muscle

Fig. 13. Posterior lip of blowhole partly cut away and folded back, and vestibular sac cut open to show its inner boundary where the plugs pass beneath the posterior wall. See Figs. 21 and 22 for transverse extent of this opening.

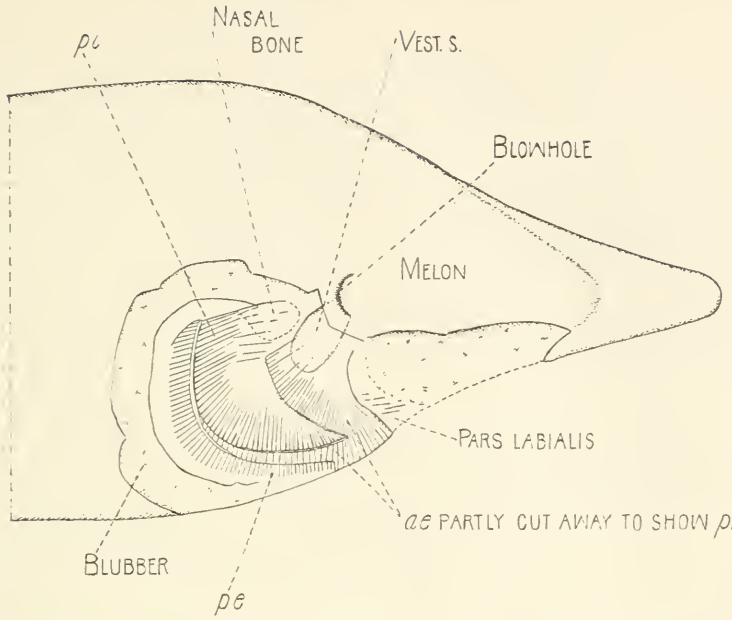

NASAL BONE
VEST. S.
BLOWHOLE
MELON
PARS LABIALIS
ae PARTLY CUT AWAY TO SHOW pi
BLUBBER
pe

Fig. 13

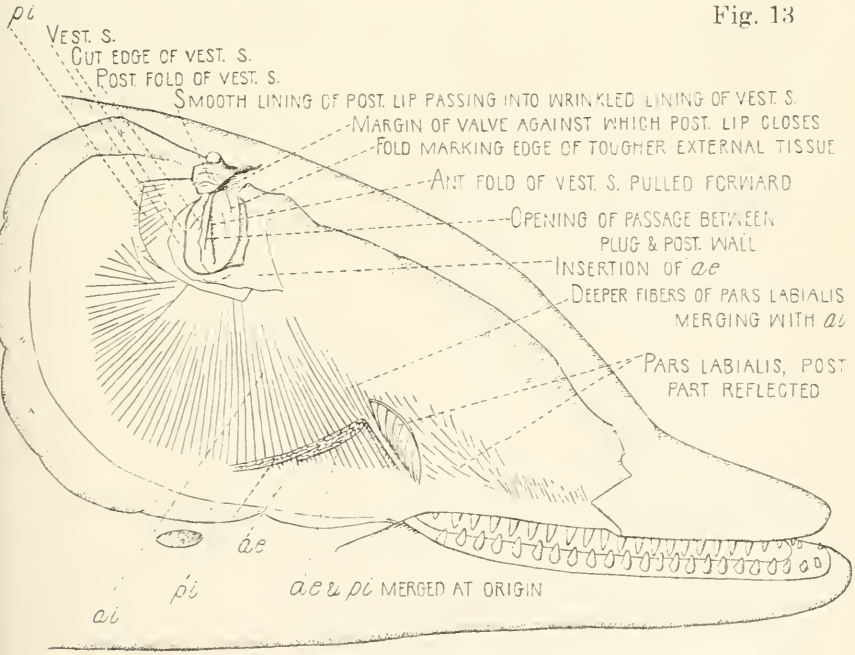

pi
VEST. S.
CUT EDGE OF VEST. S.
POST FOLD OF VEST. S.
SMOOTH LINING OF POST. LIP PASSING INTO WRINKLED LINING OF VEST. S.
MARGIN OF VALVE AGAINST WHICH POST. LIP CLOSES
FOLD MARKING EDGE OF TOUGHER EXTERNAL TISSUE
ANT FOLD OF VEST. S. PULLED FORWARD
OPENING OF PASSAGE BETWEEN PLUG & POST. WALL
INSERTION OF ae
DEEPER FIBERS OF PARS LABIALIS MERGING WITH ai
PARS LABIALIS, POST PART REFLECTED
ae
pi
ae & pi MERGED AT ORIGIN
ai

Fig. 14. Vestibular sac and folds cut away to show insertion of anterointernus and posterointernus.

Fig. 15. Posterointernus and outer part of anterointernus cut away to show tubular sac and its intrinsic muscles.

Fig. 14

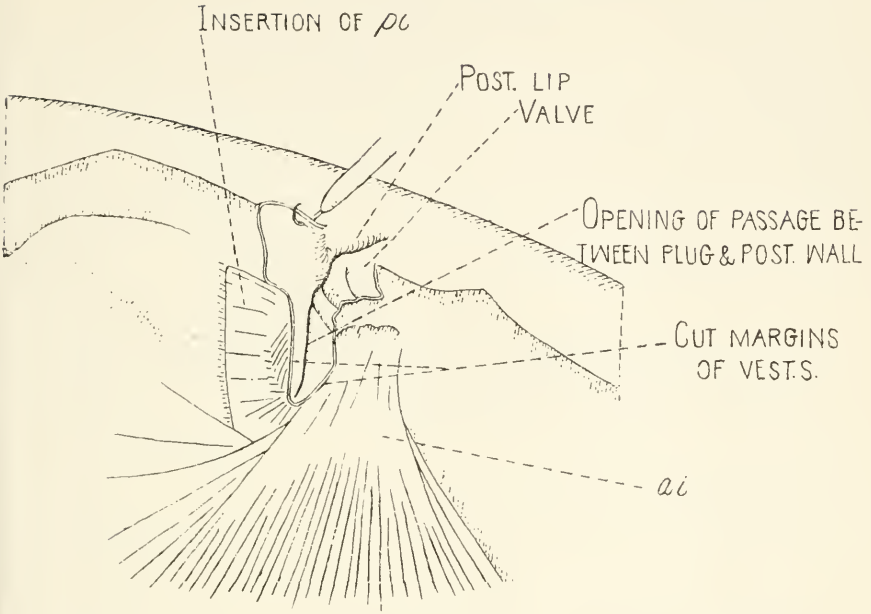

INSERTION OF pc
POST. LIP
VALVE
OPENING OF PASSAGE BE-
TWEEN PLUG & POST. WALL
CUT MARGINS
OF VEST. S.
ai

Fig. 15

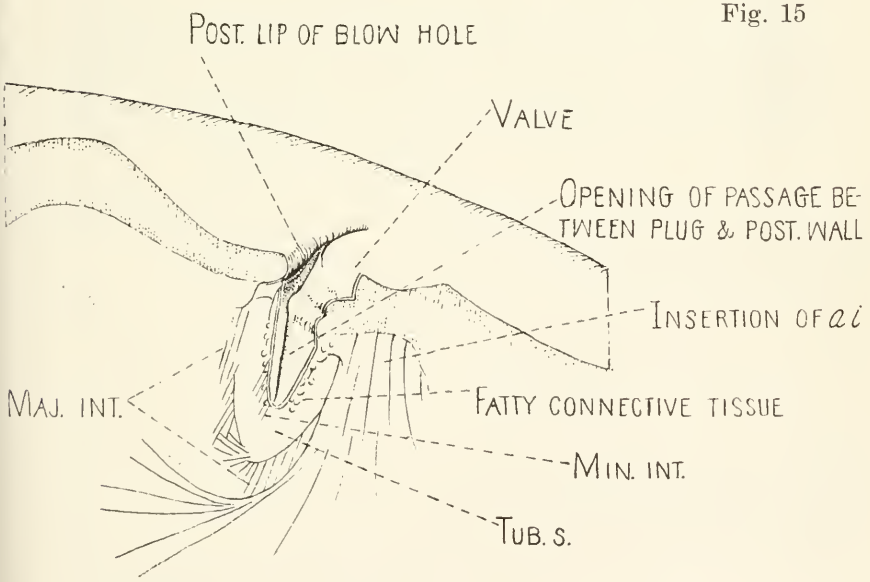

POST. LIP OF BLOW HOLE
VALVE
OPENING OF PASSAGE BE-
TWEEN PLUG & POST. WALL
INSERTION OF ai
MAJ. INT.
FATTY CONNECTIVE TISSUE
MIN. INT.
TUB. S.

Fig. 16. Tubular sac partly cut away to show connecting sac, edge of premaxillary sac, and inner part of major intrinsic muscle.

Fig. 17. Connecting sac and blowhole ligament cut away. The tubular sac is partly cut away, and its entrance pulled open to show the plug internal to it. The premaxillary sac is cut along the margin of the premaxilla and pulled open to show its relation to the tubular sac and the main passage. Two probes show respectively the opening of the tubular sac into the passage (solid line) and the lateral extent of the passage between the plug and the posterior wall (dotted line).

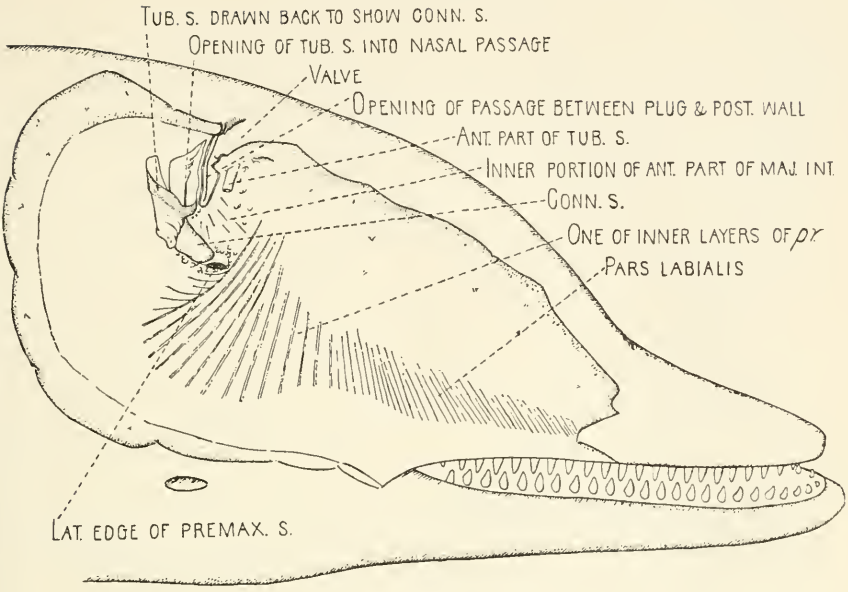

TUB. S. DRAWN BACK TO SHOW CONN. S.
OPENING OF TUB. S. INTO NASAL PASSAGE
VALVE
OPENING OF PASSAGE BETWEEN PLUG & POST. WALL
ANT. PART OF TUB. S.
INNER PORTION OF ANT. PART OF MAJ. INT.
CONN. S.
ONE OF INNER LAYERS OF pr.
PARS LABIALIS
LAT. EDGE OF PREMAX. S.

Fig. 17

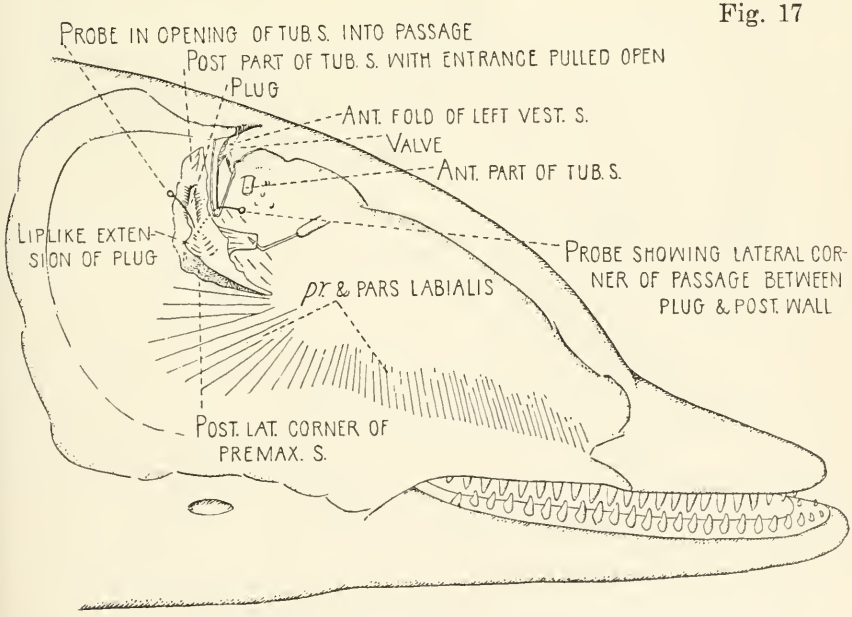

PROBE IN OPENING OF TUB. S. INTO PASSAGE
POST PART OF TUB. S. WITH ENTRANCE PULLED OPEN
PLUG
ANT. FOLD OF LEFT VEST. S.
VALVE
ANT. PART OF TUB. S.
LIP-LIKE EXTENSION OF PLUG
PROBE SHOWING LATERAL CORNER OF PASSAGE BETWEEN PLUG & POST. WALL
pr. & PARS LABIALIS
POST. LAT. CORNER OF PREMAX. S.

Fig. 18. Right half of melon cut away to show inner edge of insertion of pars labialis and its relation to profundus. The premaxillary sac lateral to the naris has been pulled open to show the diagonal membrane.

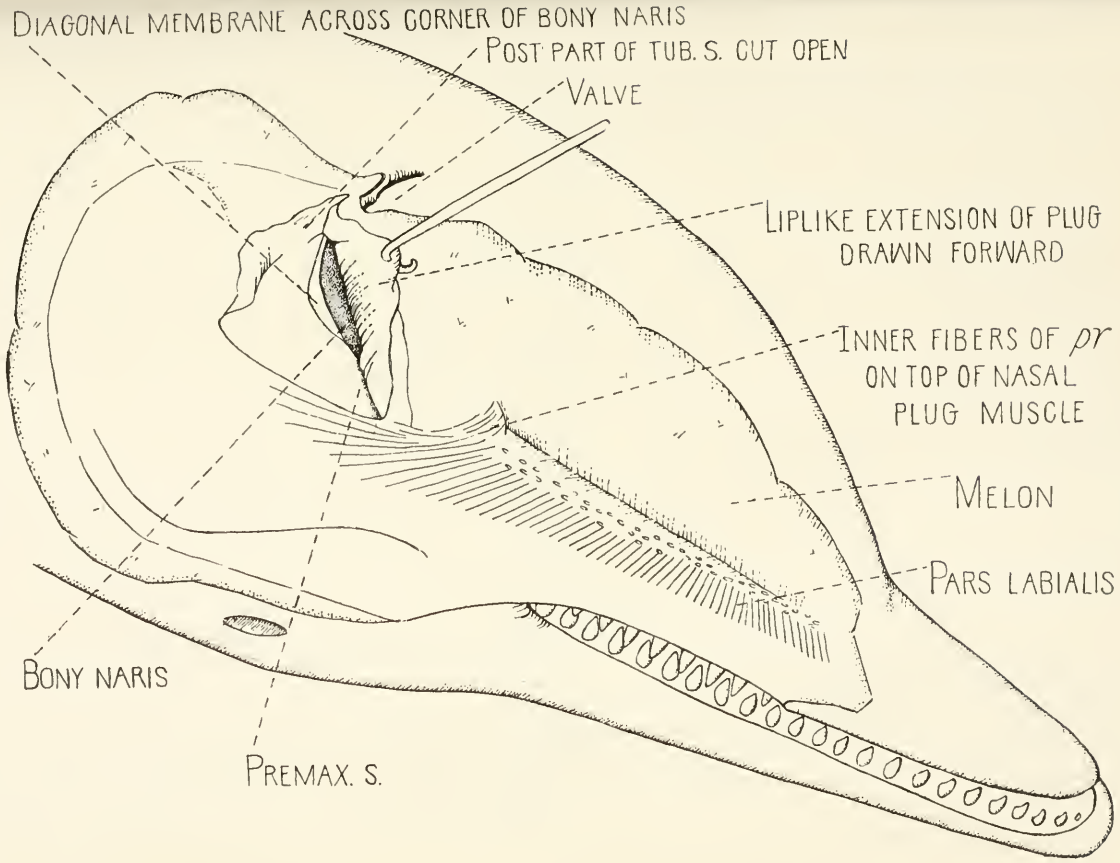

DIAGONAL MEMBRANE ACROSS CORNER OF BONY NARIS
POST PART OF TUB. S. CUT OPEN
VALVE
LIPLIKE EXTENSION OF PLUG DRAWN FORWARD
INNER FIBERS OF pr ON TOP OF NASAL PLUG MUSCLE
MELON
PARS LABIALIS
BONY NARIS
PREMAX. S.

Fig. 18

Fig. 19. Valve and plug drawn forward to show anterior and posterior limits of attachment of plug on septum and position of anterior and posterior folds of vestibular sac on left side.

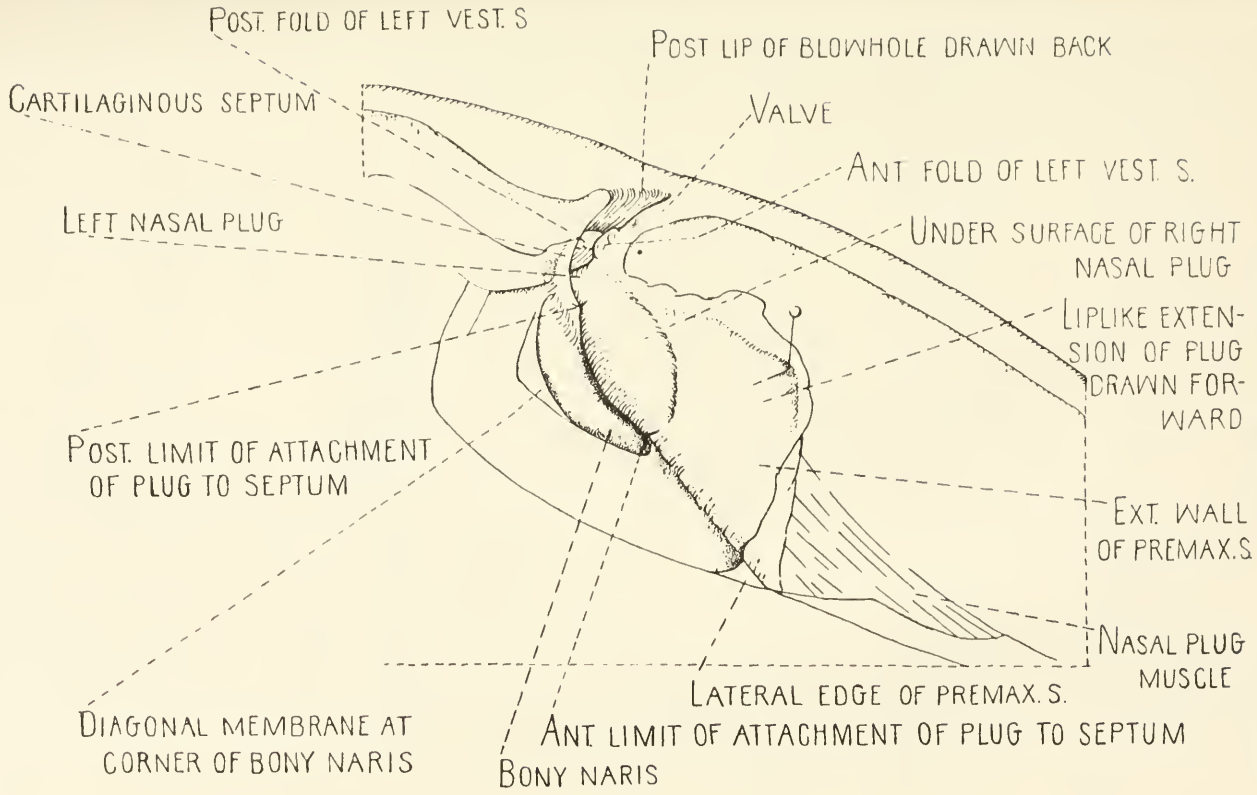

POST. FOLD OF LEFT VEST. S
POST LIP OF BLOWHOLE DRAWN BACK
CARTILAGINOUS SEPTUM
VALVE
ANT FOLD OF LEFT VEST. S.
LEFT NASAL PLUG
UNDER SURFACE OF RIGHT NASAL PLUG
LIPLIKE EXTENSION OF PLUG DRAWN FORWARD
POST. LIMIT OF ATTACHMENT OF PLUG TO SEPTUM
EXT. WALL OF PREMAX.S
NASAL PLUG MUSCLE
LATERAL EDGE OF PREMAX. S.
DIAGONAL MEMBRANE AT CORNER OF BONY NARIS
ANT LIMIT OF ATTACHMENT OF PLUG TO SEPTUM
BONY NARIS

Fig. 19

Fig. 20. Exploded diagram of the sacs cut open and distorted, to show their relation to each other and to the main passage. The outer part, constriction, and inner part have been separated as shown by arrows. Jagged lines show where the sacs have been cut open. Details of the plug and main passage are omitted, and the folds of the vestibular sac are not shown.

Outer part, *A*. This shows the vestibular sac (*vs*) as an expanded part of the passage between the valve (*v*) and the slit (*s*), where the plug (*p*) passes beneath the posterior wall (*pw*). This slit is at once part of the main passage and the inner opening of the vestibular sac. The outer opening (*o*) of the vestibular sac is at the lips of the blowhole.

Constriction, *B*. The tubular sac (*ts*) lies on each side of the slit (*s*), and its opening (*e*) is downward into the passage external to the plug. The entrance to the connecting sac (*cs*), which has been stretched open (cf. Figs. 1, 22), lies external to the liplike extension (*l*) of the plug and passes upward (*u*) to join the entrance of the tubular sac.

Inner part, *C*. The plug has been cut away medially to show the naris (*n*) and the inner opening of the premaxillary sac (*ps*) around the margin (*m*) of the premaxillary bone. Laterally the premaxillary sac has been cut, and part of the blowhole ligament (*t*) removed to show the second opening (*b*) of this sac which is into the passage external to the liplike extension (*l*) of the plug. The opening of the connecting sac (*cs*) downward into the passage in the region marked *i* has been much widened.

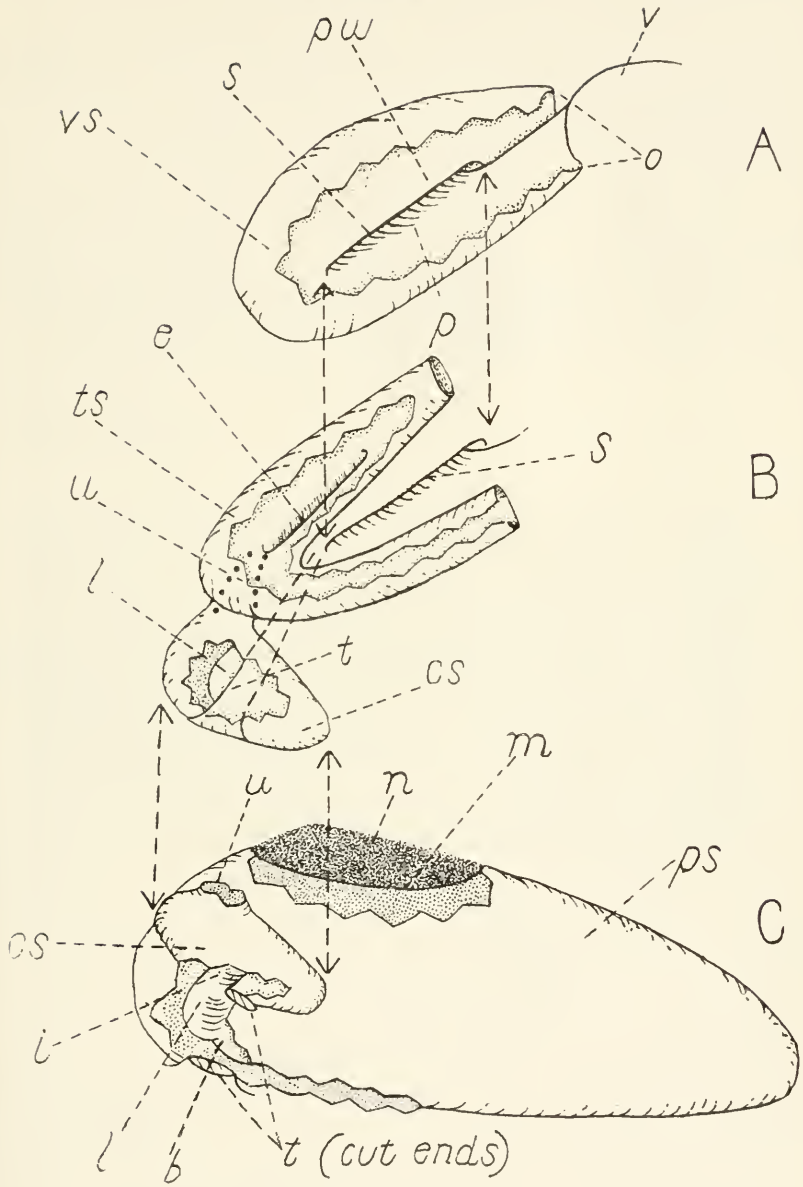

pw
v
s
vs
o
A
e
p
ts
s
B
u
l
t
cs
m
u
n
ps
C
cs
i
l
b
t (cut ends)

Fig. 21. Dorsal view of passage cut open at commissure of blowhole. Anterior fold of vestibular sac drawn forward to show transverse extent of passage at point where plugs pass beneath posterior wall.

Fig. 22. Diagram of dorsal view of passage with outer part including vestibular sac cut away. On the left side of the figure the opening where the plug passes beneath the posterior wall marks the inner limit of the vestibular area; the position of the tubular sac around this slit and the outline of the plug beneath this sac are indicated by broken lines; the connecting sac is omitted. On the right side of the figure, the posterior wall of the passage has been cut away from the skull (along irregular line) and folded forward to show the lateral entrance to the premaxillary sac. The dotted line shows the attachment of the superficial wall of the premaxillary sac external to the liplike extension of the plug. The broken line shows the margin of the plug continuous with that of the premaxillary sac. The entrance to the connecting sac (as well as the sac, which is not shown) is very much smaller on this side than on the right (cf. Fig. 1).

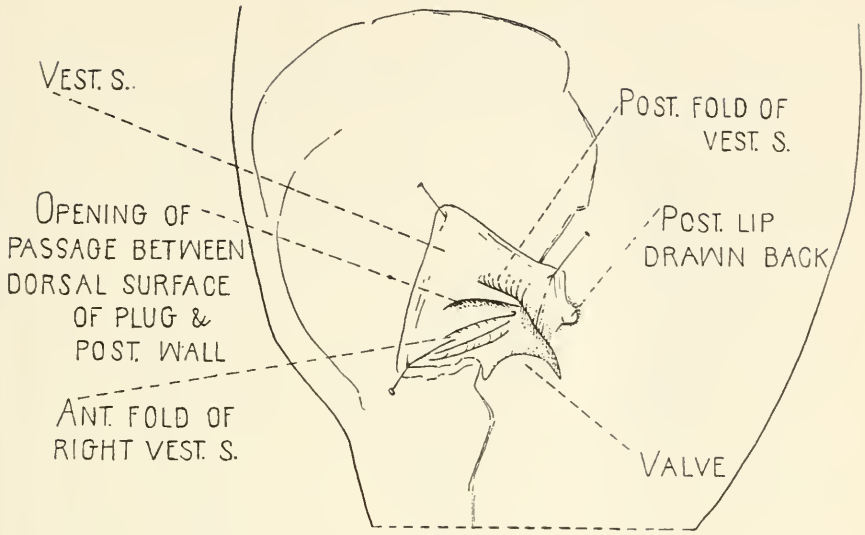

VEST. S.
POST. FOLD OF VEST. S.
OPENING OF PASSAGE BETWEEN DORSAL SURFACE OF PLUG & POST. WALL
POST. LIP DRAWN BACK
ANT. FOLD OF RIGHT VEST. S.
VALVE

Fig. 22

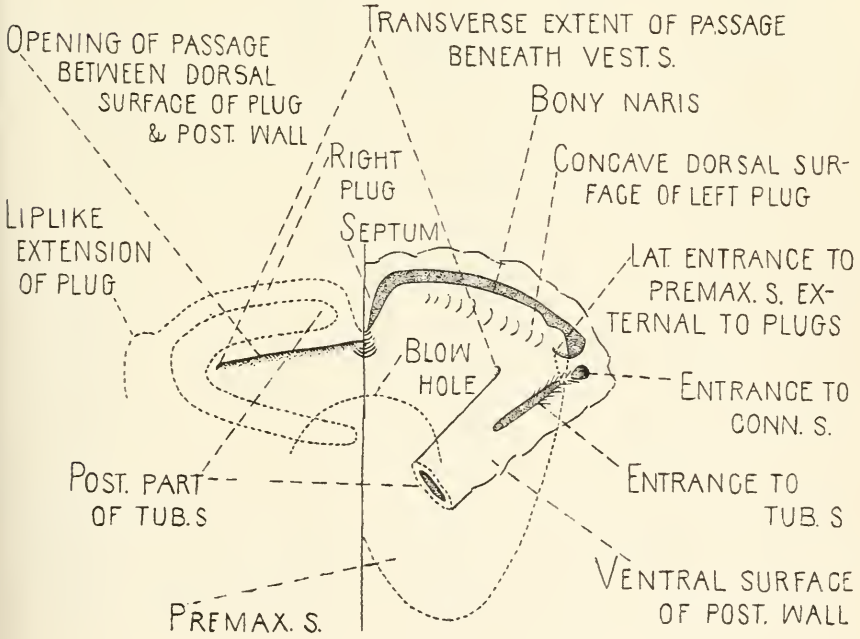

OPENING OF PASSAGE BETWEEN DORSAL SURFACE OF PLUG & POST. WALL
TRANSVERSE EXTENT OF PASSAGE BENEATH VEST. S.
BONY NARIS
RIGHT PLUG
CONCAVE DORSAL SURFACE OF LEFT PLUG
LIPLIKE EXTENSION OF PLUG
SEPTUM
LAT. ENTRANCE TO PREMAX. S. EXTERNAL TO PLUGS
BLOW HOLE
ENTRANCE TO CONN. S.
POST. PART OF TUB. S
ENTRANCE TO TUB. S
VENTRAL SURFACE OF POST. WALL
PREMAX. S.

Fig. 23. Dorsal view of skull showing muscle attachments (on left of figure), and arrangement of bones around nares.

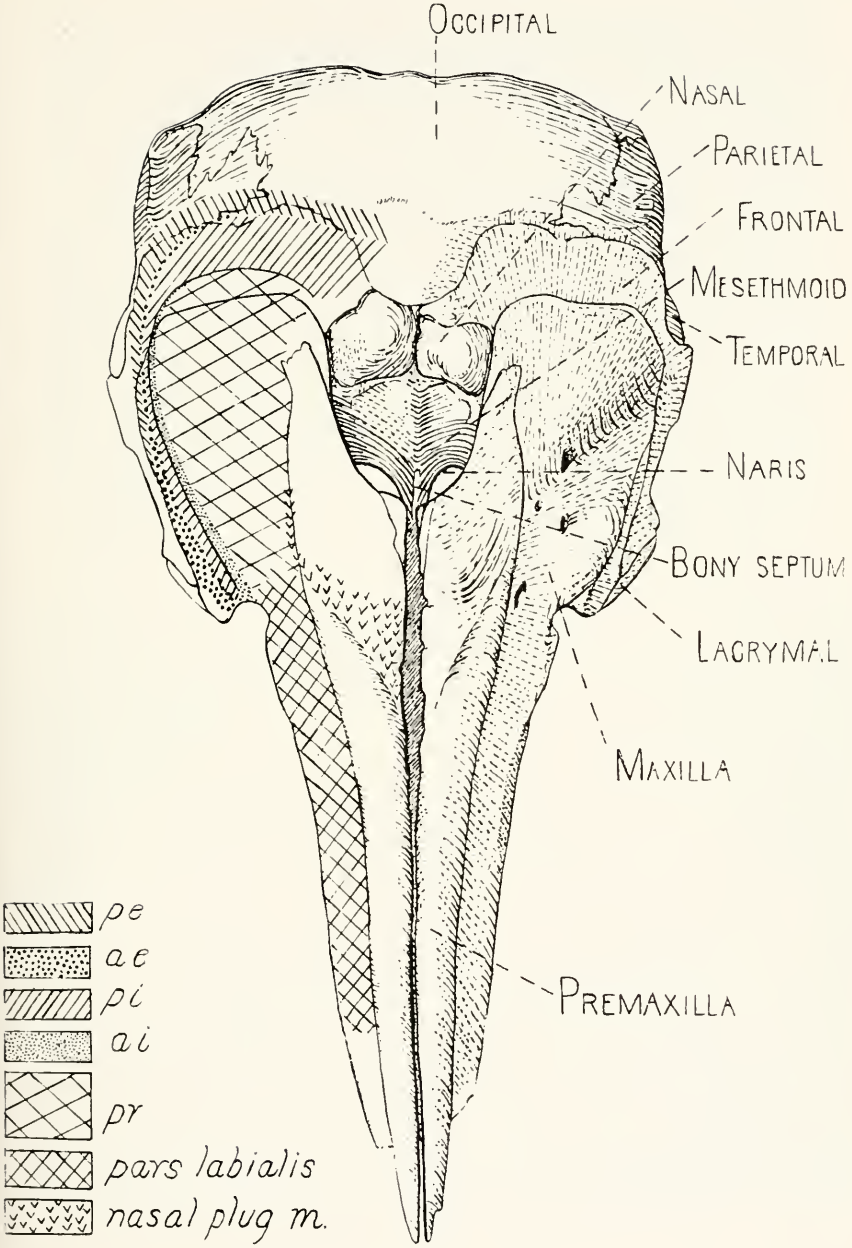
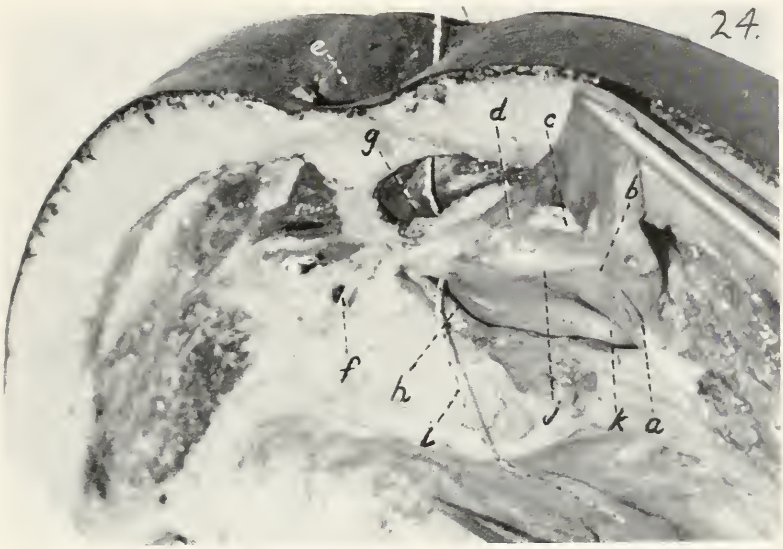

OCCIPITAL
NASAL
PARIETAL
FRONTAL
MESETHMOID
TEMPORAL
NARIS
BONY SEPTUM
LACRYMAL
MAXILLA
PREMAXILLA
pe
ae
pi
ai
pr
pars labialis
nasal plug m.

Fig. 24. Photograph of rostral face of section at *a*, Fig. 6. The cuts indicated in Fig. 7 have been made and pulled open to show liplike extension of plug and entrance to connecting sac as well as the interior of the posterior part of the tubular sac. The string following the passage outward is hidden as it passes between the dorsal surface of the plug and the concave mass of the posterior wall, visible as it passes around the anterior fold of the vestibular sac, and hidden again till it emerges from blowhole. Abbreviations: *a*, paper marker at entrance to connecting sac; *b*, lateral end of opening of tubular sac into passage; *c*, paper marker in bend leading to anterior part of tubular sac; *d*, interior of posterior part of tubular sac; *e*, valve, or anterior lip of blowhole; *f*, diagonal membrane in left side of passage; *g*, anterior fold of vestibular sac; *h*, passage beneath plug; *i*, string entering passage superficial to plug; *j*, anterior margin of opening of tubular sac; *k*, liplike extension of plug.

Fig. 25. Rostral face of section through melon made at *d*, Fig. 6, showing insertions of pars labialis and the gradual transition from the more oily melon to the more fibrous blubber. Abbreviations: *m*, melon; *n*, blubber; *o*, rostrum; *p*, pars labialis.


24.
e
g
d
c
b
f
h
i
j
k
a

25.
m
n
p
o

Fig. 26. Beginning of blow. Alternate frames from pictures taken at 64 frames per second looking into left side of passage as it opens. In this and Figures 27 and 28 the following abbreviations are used:

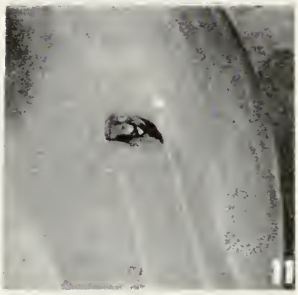
b, bony wall of naris; *c*, convex mass of posterior wall;
d, diagonal membrane; *f*, anterior fold of vestibular sac;
l, liplike extension of plug; *p*, plug; *s*, septum; *v*, valve.

Here as well as in the following sequences (Figs. 27-30), anterior is at the bottom of the picture, posterior at the top. In this sequence in the fifth frame the edge of the diagonal membrane shows internal to the convex mass; as the blowhole aperture widens, the liplike extension of the plug appears as a pale mass external to the diagonal membrane in the lower left hand corner of the open passage (frames 11, 13, and 15).

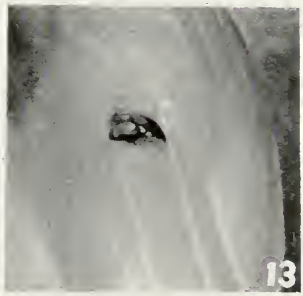
1

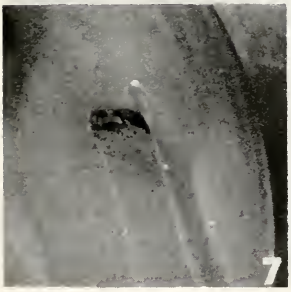
9

3


11

c
S
V
5


13


7

b
c
a
S
V
I
15

Fig. 27. End of blow begun in Figure 26. Uninterrupted sequence of frames from pictures taken at 64 frames per second looking into passage a little to left of midline. As it closes, first the plugs (frame 3), then the anterior fold of the vestibular sac (frame 4), and last the valve are seen falling into place one after the other. The asymmetrical closing as well as the positions of the septum and concave mass of the posterior wall show clearly.

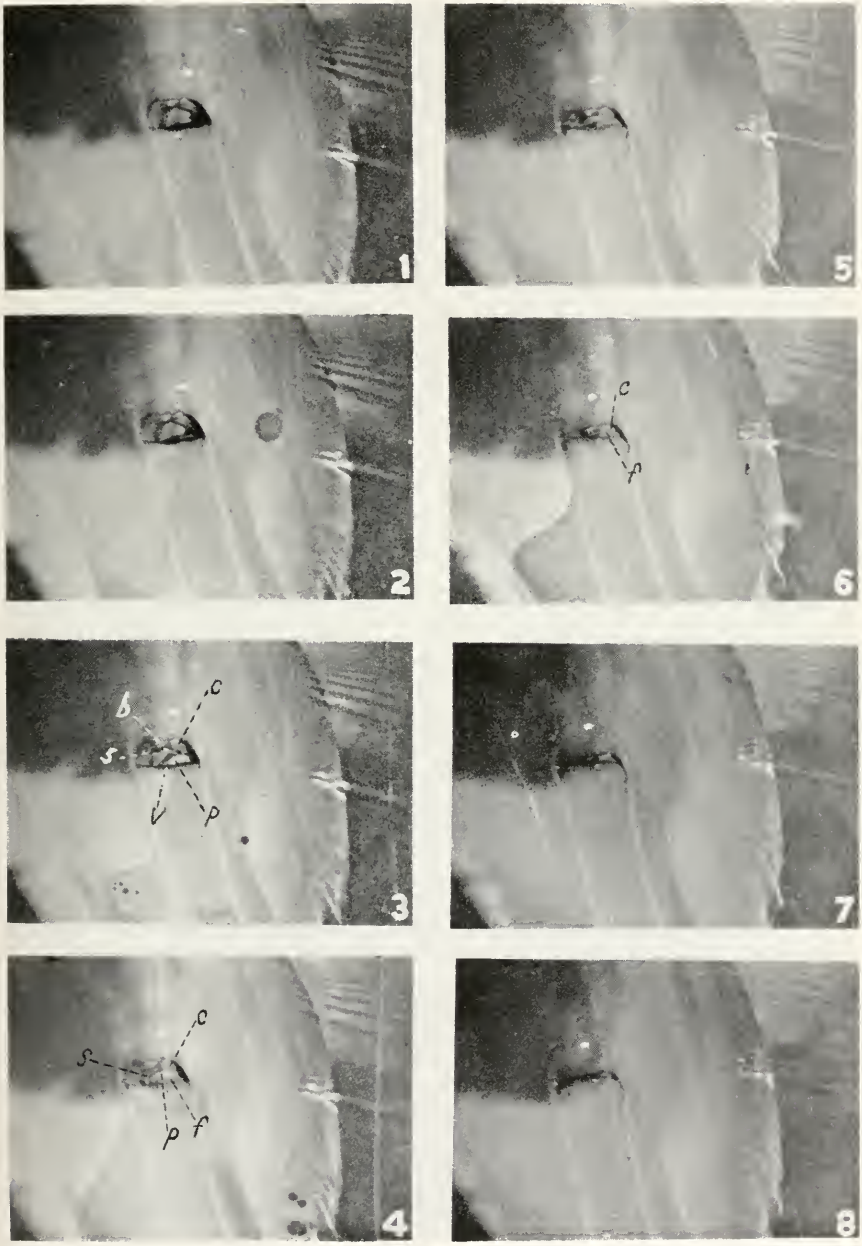
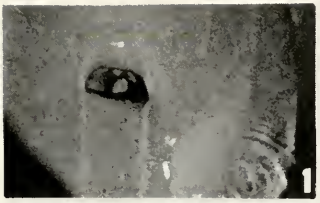
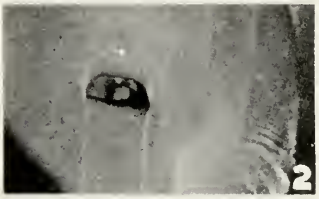

1
2
3
b
c
s
p
4
c
s
p
f
5
6
c
f
7
8

Fig. 28. Slightly different view of blowhole closing, showing more of right half of passage. The frames are in uninterrupted sequence and were taken at 64 frames per second. The outer shadow in the left side of the passage (see especially frames 1-4) marks the entrance to the vestibular sac; the inner shadow is in the naris internal to the convex mass of the posterior wall. The fourth frame shows the plug closing beneath this mass. The sixth, seventh, and eighth frames show the anterior fold of the vestibular sac closing on top of this mass.


1

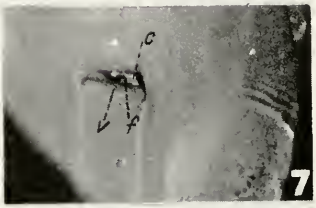

2

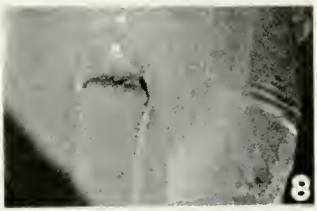
b
c
s
3

p
4

c
s
p
f
5

6


c
p
f
7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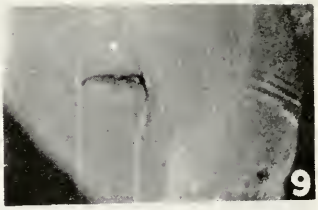

9

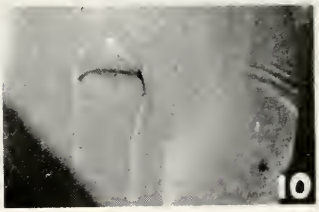

10

Fig. 29. Uninterrupted sequence of frames from pictures taken at 64 frames per second showing water running into open blowhole as porpoise submerges, and low spray as some water is forced back out.

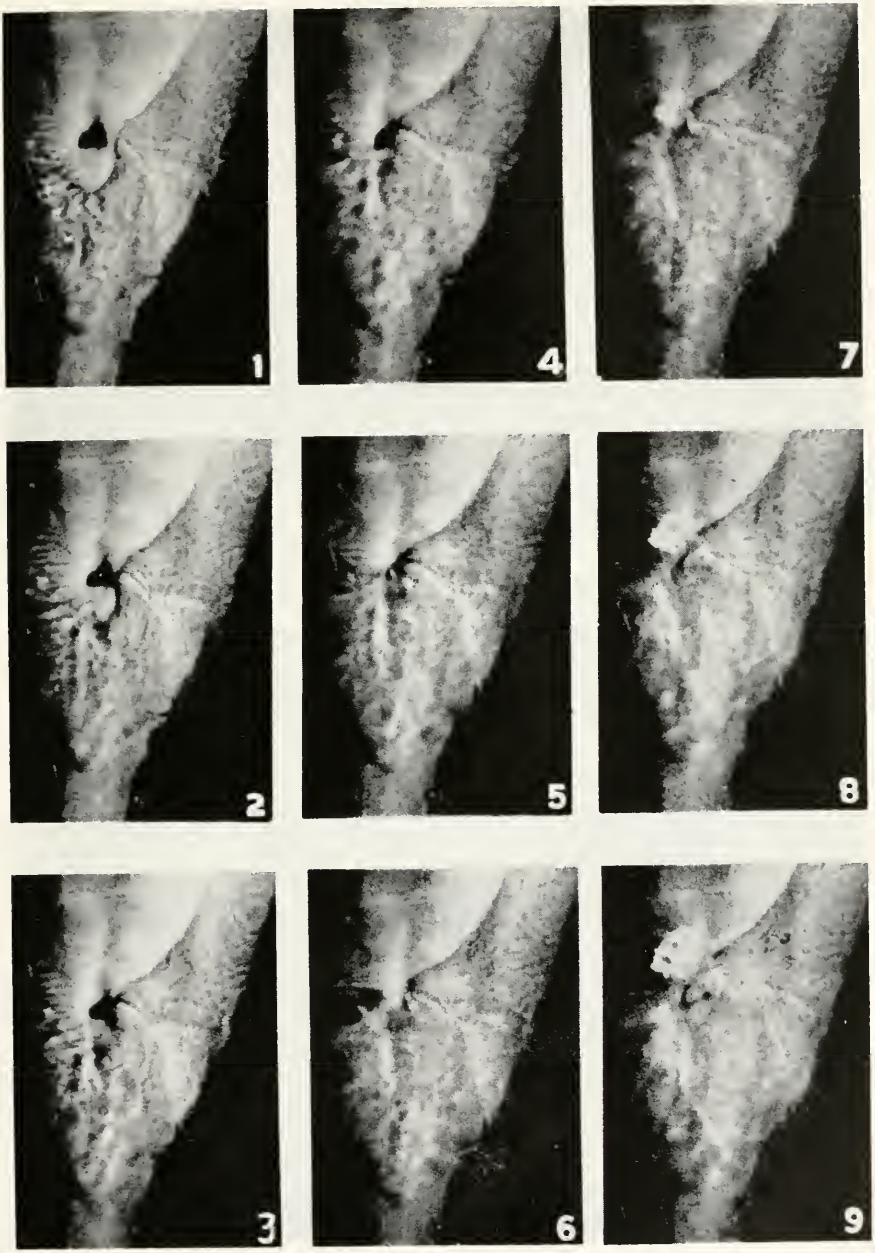
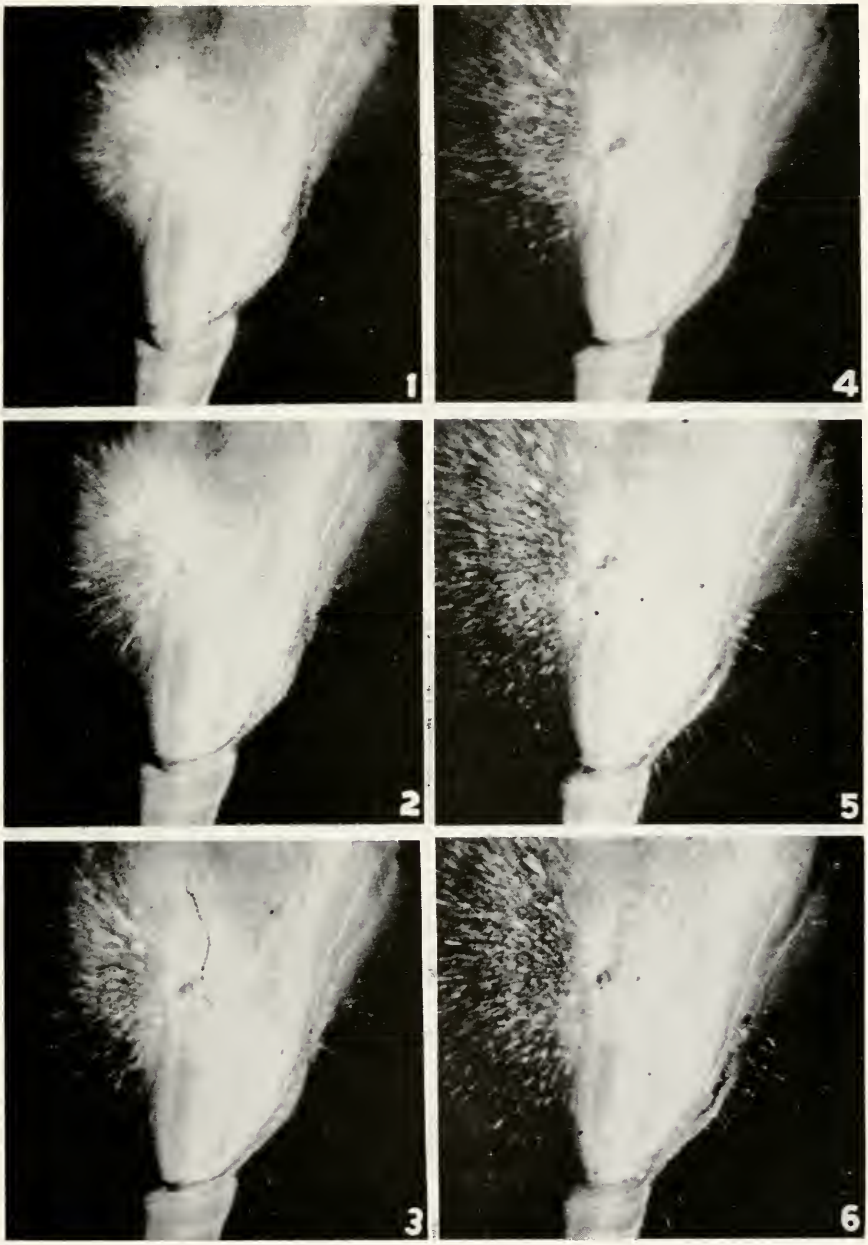

1
4
7
2
5
8
3
6
9

Fig. 30. Uninterrupted sequence of frames from pictures taken at 64 frames per second showing wet blow following submergence with blowhole open.


1
4
2
5
3
6

Bulletin of the Museum of Comparative Zoology
AT HARVARD COLLEGE
Vol. 114, No. 5

SILICIFIED MIDDLE ORDOVICIAN TRILOBITES: THE ODONTOPLEURIDAE

By H. B. Whittington

With Twenty-four Plates

CAMBRIDGE, MASS., U. S. A.
PRINTED FOR THE MUSEUM
May, 1956

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with the

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May, 1956

No. 5 — *Silicified Middle Ordovician trilobites: The Odontopleuridae*

By

H. B. Whittington

CONTENTS

	Page
Introduction and acknowledgements	159
Terminology	160
Stratigraphical occurrence and localities	162
Part I: Morphology, Ontogeny and Evolution	166
Morphology of holaspid exoskeleton	166
Cephalon	166
Thorax	173
Pygidium	175
External surface	175
Abnormal specimens	178
Ontogeny	178
Locus of segmental divisions	182
Mode of life	185
Origin and evolution	186
Part II: Systematic Descriptions	193
Family Odontopleuridae Burmeister	193
Discussion of systematics of Odontopleuridae	194
Subfamily Odontopleurinae Burmeister	195
Odontopleura Emmrich	196
Primaspis R. and E. Richter	198
P. ascitus n. sp.	199
Leonaspis R. and E. Richter	205
Diacanthaspis Whittington	207
D. cooperi Whittington	211
D. lepidus n. sp.	216
D. secretus n. sp.	220
Discussion of ontogeny of *Diacanthaspis*	224
D. ulrichi n. sp.	225
D. aff. *ulrichi* n. sp.	228
D. orandensis n. sp.	228
D. scitulus n. sp.	230

Page

Acidaspis Murchison 232
Dudleyaspis Prantl and Přibyl 234
Radiaspis R. and E. Richter 235
Subfamily Miraspinae R. and E. Richter . . . 235
Miraspis R. and E. Richter 236
?M. sp. ind. 238
Ceratocephala Warder 238
C. laciniata Whittington and Evitt . . . 239
C. rarispina n. sp. 242
C. (*Ceratocephalina*) n. subgen. 243
C. (*C.*) *tridens* n. sp. 244
Proceratocephala Prantl and Přibyl . . . 247
Whittingtonia Prantl and Přibyl 248
Dicranurus Conrad 248
Notes on other miraspinid genera 248
?Subfamily Miraspinae R. and E. Richter . . . 250
Odontopleurid protaspis 250
Subfamily Apianurinae n. subfam. 252
Apianurus n. gen. 252
A. barbatus n. sp. 254
Specimens at localities 2 and 3 differing from *A. barbatus* n. gen., n. sp., ... 265
A. glaber n. sp. 268
A. sp. ind. 269
A. aff. *furcata* Linnarsson 270
Calipernurus n. gen. 271
C. insolitus n. sp. 273
Subfamily Selenopeltinae Corda 279
Selenopeltis Corda 279
Other genera, subgenera and species sometimes referred to Odontopleuridae 282
References 283
Explanation of Plates 1-24 289

ILLUSTRATIONS

Plates

Plate

1. *Primaspis ascitus* n. sp. . . . . .

Plate

2. *Primaspis ascitus* n. sp. . . . . .
3. *Diacanthaspis cooperi* Whittington . . .
4. *Diacanthaspis lepidus* n. sp. . . . .
5. *Diacanthaspis lepidus* n. sp. . . . .
6. *Diacanthaspis secretus* n. sp. . . . .
7. *Diacanthaspis secretus* n. sp. and *D. lepidus* n. sp. . . . . .
8. *Diacanthaspis ulrichi* n. sp. . . . .
9. *Diacanthaspis* aff. *ulrichi* n. sp. and *D. cooperi* Whittington . . . . . .
10. *Diacanthaspis orandensis* n. sp. . . .
11. *Diacanthaspis orandensis* n. sp. and *D. cooperi* Whittington . . . . . .
12. *Diacanthaspis scitulus* n. sp. . . . .
13. *Diacanthaspis scitulus* n. sp. . . . .
14. *Miraspis* sp. ind. and *Ceratocephala laciniata* Whittington and Evitt . . . . .
15. *Ceratocephala rarispina* n. sp. and *C.* (*Ceratocephalina*) n. subgen., sp. ind. . . .
16. *Ceratocephala* (*Ceratocephalina*) *tridens* n. subgen., n. sp. . . . . .
17. *Apianurus barbatus* n. gen., n. sp. . . .
18. *Apianurus barbatus* n. gen., n. sp. . . .
19. *Apianurus barbatus* n. gen., n. sp. . . .
20 *Apianurus barbatus* n. gen., n. sp., and *A.* aff. *furcata* Linnarsson . . . . .
21. *Apianurus glaber* n. gen., n. sp., *Apianurus* n. gen., sp. ind., and miraspinid ? protaspis .
22. *Calipernurus insolitus* n. gen., n. sp. . .
23. *Calipernurus insolitus* n. gen., n. sp. . .
24. *Calipernurus insolitus* n. gen., n. sp. . . .

Figures

Figure *Page*

1. Notation for spines of Stage 0 cranidium . . 161
2. Hypostomes characteristic of subfamilies . . 171
3. Classification, relationships, range in time of Odontopleuridae 188–189

Figure		*Page*
4.	*Odontopleura ovata* Emmrich	197
5.	*Primaspis primordialis* (Barrande)	198
6.	Development of *Primaspis ascitus* n. sp.	204
7.	*Leonaspis* n. sp.	206
8.	Age and comparison of species of *Diacanthaspis*	208-209
9.	Development of *Diacanthaspis cooperi* Whittington	213
10.	Reconstruction of *Diacanthaspis lepidus* n. sp.	218
11.	Development of *Diacanthaspis secretus* n. sp.	222
12.	Development of *Diacanthaspis ulrichi* n. sp.	227
13.	*Acidaspis brightii* Murchison	233
14.	*Dudleyaspis quinquespinosa* (Lake)	234
15.	*Miraspis mira* (Barrande)	237
16.	*Ceratocephala laciniata* Whittington and Evitt	239
17.	*Whittingtonia bispinosa* (M'Coy)	247
18.	*Dicranurus monstrosus* (Barrande)	249
19.	Reconstruction of *Apianurus barbatus* n. gen., n. sp.	253
20.	Cephalon of *Apianurus barbatus* n. gen., n. sp.	256
21.	Triangular graph of dimensions of *Apianurus barbatus* n. gen., n. sp.	259
22.	Development of *Apianurus barbatus* n. gen., n. sp.	261
23.	Triangular graph of dimensions of *Apianurus barbatus* n. gen., n. sp., and *Calipernurus insolitus* n. gen., n. sp.	272
24.	Reconstruction of *Calipernurus insolitus* n. gen., n. sp.	274
25.	*Selenopeltis buchi* (Barrande)	281

Tables

Table		*Page*
1.	Numbers of exoskeletal parts of two species of *Diacanthaspis* at localities 2-4	217
2.	Numbers of exoskeletal parts of three species of *Diacanthaspis* at locality 8	229
3.	Numbers of odontopleurid cranidia at locality 8	242
4.	Numbers of exoskeletal parts of all sizes of *Apianurus* n. gen., and *Calipernurus* n. gen.	267

INTRODUCTION AND ACKNOWLEDGEMENTS

The photographs show the remarkable nature of the silicified material from Virginia — superbly preserved, free from the matrix, undistorted, and including adults and growth stages. These specimens afford a detailed picture of an early part of the history of odontopleurid trilobites, and thus throw new light on the morphology and evolution of the family. The best odontopleurid material previously known was that described by Barrande (1852, 1872) and recently re-studied by Prantl and Přibyl (1949). Although these Bohemian odontopleurids range in age from Ordovician to Devonian, they are not as well preserved, nor are growth stages known. It is my good fortune that the Museum of Comparative Zoology houses the Schary Collection (to which Barrande originally had access), for this circumstance enabled me to study the Bohemian species at first hand. A visit to Britain in 1953, and generous loans from American museums, have permitted me to see additional specimens. The type and certain other species have been described elsewhere (Whittington, 1956b), and two silicified species from Virginia were treated of by Whittington and Evitt (1954). In Part II of this paper the remainder of the silicified odontopleurids are described in detail. In Part I, the morphology, ontogeny, and evolution of the family are discussed in general terms. Part II embodies a classification arising out of the new data, and my views on evolution, and includes notes on all the genera which have been referred to the Odontopleuridae.

The amount of morphological detail which the silicified exoskeletons reveal enables fine distinctions to be drawn between genera and between species, i.e. it encourages "splitting." Examples are the new subgenus *Ceratocephala* (*Ceratocephalina*), the differences between *Apianurus* n.gen. and *Calipernurus* n.gen., and between some of the species of *Diacanthaspis*. On the other hand, the seven species of *Diacanthaspis* seem to form part of a natural, related group, and I have widened the original diagnosis of *Diacanthaspis* rather than split it into subgeneric groups. In dealing with the less well-preserved and often incomplete material on which some Ordovician and all later genera have been established, I have tended to "lump" rather than

"split." Thus, widely varying degrees of morphological difference separate the genera shown in Text-figure 3, and these differences are not of equal rank.

Dr. G. Arthur Cooper and his colleagues at the U. S. National Museum first discovered silicified trilobites in the Middle Ordovician limestones of Virginia about 1935. In succeeding years a large collection was prepared, and in 1946 Dr. Cooper invited me to study it, under project grant 491-46 from the Penrose Bequest of the Geological Society of America. Meanwhile, Dr. William R. Evitt, University of Rochester, independently discovered these fossils, and since 1947 he and I have collaborated in the preparation of additional material and in studies of it. The silicified trilobites here described are thus derived from our own as well as U. S. National Museum collections. A special debt of gratitude is owed to Mrs. Evitt for her painstaking sorting of the finest residues, which brought to light many of the tiny growth stages. I am also grateful to Mrs. Stanley J. Olsen, Mrs. Robert E. Kay, and Mr. Ira B. Laby for preparing the enlargements from my negatives and for aiding in mounting the plates. Text-figures 10 and 19 were drawn from my sketches by Mr. F. Y. Cheng, the remainder by Miss Pat Washer. Professor L. Størmer, Paleontological Institute, Oslo, kindly permitted me to describe a Norwegian species here.

TERMINOLOGY

The terminology used herein is the same as that employed by Whittington and Evitt, 1954, pp. 11-14, with certain additions and emendations:—

Cephalic spines: to simplify description of cephalic spines a system of letters and numbers has been adopted (Text-fig. 1). Median or paired *axial spines* of the glabella have been numbered 1-5, commencing with the median occipital and numbering forwards; 2a is an additional pair appearing later in the ontogeny than 1 and 2. These numbers do not correspond with those used by Whittington and Evitt (1954, text-fig. 16), where 2a is numbered 2, 2 is 3, 3 is 4, etc. Certain *paired cheek spines* have been lettered as shown. In the protaspis and Stage 0 cephala of *Diacanthaspis* (Text-figs. 9, 11, 12) and *Apianurus* n. gen. (Text-fig. 22) there is a long, backwardly-directed spine

at the extremity of the posterior border of the fixed cheek, as well as a long spine on the border of the free cheek. These spines have been called *fixigenal* and *librigenal* respectively (terms proposed by Richter, 1932), in preference to the older terms metacranidial and parial of Raw (1925).

Antennular notch: a notch in the margin of the free cheek immediately outside the anterior branch of the facial suture (*a* in Text-fig. 20; see also Pl. 1, figs. 2, 5; Pl. 17, figs. 7, 10). As

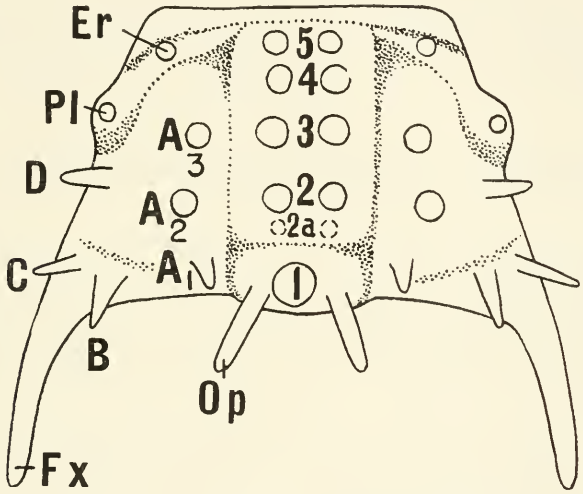


Figure 1. Cranidium of Stage 0 odontopleurid based on that of *Apianurus barbatus* n.gen., n.sp., with paired spines numbered and lettered as follows: 1, 2a, 2, 3, 4, 5, six pairs of axial glabellar spines numbered forward from the occipital ring; A_1, A_2, A_3, on fixed cheek; B, C, on posterior border; D, on fixed cheek behind palpebral lobe; Er, on eye ride; Fx, fixigenal; Op, paired occipital spine; Pl, on summit of palpebral lobe.

explained under "Cephalon: hypostome" and "Mode of Life," this notch may permit the antennule to protrude forward when the animal is resting on the sea bottom.

Pleural spines: The pleura may be divided by a pleural furrow into a convex anterior and posterior band, and each of these bands may be prolonged distally into a spine (the anterior into more than one spine), here called *anterior pleural* (not terminal

of Prantl and Přibyl, 1949, p. 128) and *posterior pleural* spines respectively.

Pleural region is used for that part of the pygidium outside the axis, rather than pleural lobe.

Pygidial spines: Commonly one paired spine is longer and stouter than the others, and is here called the *major* spine; it may arise from the border or the surface of the pleural region, and the base is always connected to the first axial ring by a low ridge, here termed the *pleural ridge.*

Sagittal (*sag.*), *Exsagittal* (*exs.*), and *Transverse* (*tr.*) refer respectively to the median line, a line parallel to, but outside of the median, and a direction at right angles to the median. The abbreviations used in the text are given in parentheses.

STRATIGRAPHICAL OCCURRENCE AND LOCALITIES

The specimens described here were obtained from limestones of the Edinburg, Oranda and Martinsburg formations of the Shenandoah Valley, northern Virginia. The stratigraphy of these formations has been described by Cooper and Cooper (1946), and the classification and correlation is summarized in Twenhofel *et al.* (1954). Trilobites from the Edinburg and underlying limestones have been described by Evitt (1951), Cooper (1953), and Whittington and Evitt (1954), and the latter work also contains an account of the mode of occurrence, preservation, and method of extraction of the silicified specimens. Trilobites from the lower Martinsburg formation have been described by Whittington (1941), Evitt (1953) and Evitt and Whittington (1953). Odontopleuridae first appear in the lower Lincolnshire limestone (*Ceratocephala triacantheis* Whittington and Evitt and fragments of *Apianurus* n. gen.), below the Edinburg formation. In the lowest part of the latter formation (localities 2-4) they are abundant and exhibit the greatest variety. In the slightly higher horizon at locality 6 odontopleurids are rare, but they become numerous and varied again some 400 feet higher in the section in the Oranda formation. The latter is not more than 50 ft. thick, and in the lowest part of the succeeding Martinsburg formation silicified odontopleurids again occur in fair abundance and variety. Not all the blocks of

limestone collected yield good material, and the same species do not appear at different localities in the same formation — perhaps because of slight differences in horizon. Thus *Diacanthaspis ulrichi* n. sp. is the only odontopleurid at the lower Edinburg locality 7, is rare at locality 4, and unknown at 2 and 3. *Primaspis ascitus* n. sp. is only known at locality 10 in the lower Martinsburg, and does not accompany *D. cooperi* at localities 9, 11 and 12.

The localities (cf. Whittington and Evitt, 1954, pp. 5-6) and the odontopleurids obtained at each are listed below. Tables 1-4 give numbers of specimens recovered of particular species.

Edinburg limestone

Locality 2 — Lower part of Edinburg limestone (bed 18 of Cooper and Cooper, 1946, geologic section 19, pp. 94-95), yellowish-weathering argillaceous limestone forming edge of quarry and along strike of same bed, in field between quarry and railroad; just north of railroad tracks at switch a quarter of a mile east of Strasburg Junction, just west of Strasburg, Shenandoah County, Virginia. Some of the finest specimens illustrated here came from blocks collected at this locality and prepared by Dr. G. Arthur Cooper.

Diacanthaspis lepidus n. sp.
Diacanthaspis secretus n. sp.
Ceratocephala laciniata Whittington and Evitt, 1954
Apianurus barbatus n. gen., n. sp.
Apianurus glaber n. gen., n. sp.
Apianurus sp. ind.
Calipernurus insolitus n. gen., n. sp.

Locality 3 — Lower part of Edinburg limestone, section in field on south side of road, 0.2 mile east of Strasburg Junction, just west of Strasburg, Shenandoah County, Virginia. The section dips about 38° SE. The lowest beds were 6 feet of granular limestones with *Girvanella* sp., about 91 feet from the east edge of the quarry dump at the top of the field. These may be upper Lincolnshire limestone. About 20 feet stratigraphically higher, alternations of dark granular limestone and dark fine-grained limestone with sponge spicules were seen. These beds seem to be

the basal Botetourt limestone member of the Edinburg formation (Cooper and Cooper, 1946, p. 80), and blocks from them were collected and prepared by Dr. G. Arthur Cooper, Dr. and Mrs. W. R. Evitt, and Whittington. These yielded all the species known from locality 2 except *Apianurus* sp. ind. In addition *Miraspis* sp. ind. and *Ceratocephala* (*Ceratocephalina*) *tridens* n. subgen., n. sp., occur.

Locality 4 — Botetourt member, lower part of Edinburg limestone, in upper part of field northeast of Virginia State Highway 639, at a point 0.25 mile from its junction with U.S. Highway 11. This junction is 0.7 mile southwest of Strasburg, Shenandoah County, Virginia. The outcrop is approximately half a mile southwest of locality 3 along the strike of the beds. Collected and prepared by Dr. and Mrs. W. R. Evitt and by Whittington, and notable for yielding some of the finest tiny specimens.

Diacanthaspis lepidus n. sp.
Diacanthaspis secretus n. sp.
Diacanthaspis ulrichi n. sp.
Ceratocephala laciniata Whittington and Evitt, 1954
Ceratocephala (*Ceratocephalina*) *tridens*, n. subgen., n. sp.
Apianurus barbatus n. gen., n. sp.
Apianurus glaber n. gen., n. sp.

Locality 6 — Edinburg limestone, lower part, Hupp Hill, at entrance to Battlefield Crystal Caverns, and in field on opposite (east) side of U. S. Highway 11, about 1½ miles north of Strasburg, Shenandoah County, Virginia. Discovered by Dr. G. Arthur Cooper, later collections by Whittington. Odontopleurids are rare, only one or two parts of exoskeletons of the following being known:—

Diacanthaspis secretus n. sp.
Ceratocephala laciniata Whittington and Evitt, 1954
Apianurus barbatus n. gen., n. sp.

Locality 7 — Lower part of Edinburg limestone, 300 feet ± south 40° east of bridge, 1¼ miles east of Edinburg, Shenandoah County, Virginia. Originally collected by E. O. Ulrich, later (1931) by Charles Butts, and yielding only one odontopleurid, *Diacanthaspis ulrichi* n. sp.

Oranda formation

Locality 8 — Lower 5 feet of formation, cobbly limestone, in bank and pasture on north side of Virginia secondary highway 777, just west of its junction with Virginia secondary highway 910, and *circa* 300 yards north of Greenmount church, five miles north of Harrisonburg, Rockingham County, Virginia. Discovered by G. Arthur Cooper, later collections by Cooper and A. R. Loeblich, Jr., W. R. Evitt, and Whittington.

Diacanthaspis orandensis n. sp.
Diacanthaspis scitulus n. sp.
Diacanthaspis aff. *ulrichi* n. sp.
Ceratocephala rarispina n. sp.
Apianurus barbatus n. gen., n. sp.

Martinsburg shale

Locality 9 — Road cut, gutter, and loose blocks in pasture on west side of Virginia secondary highway 910, about half a mile north of Greenmount church, five miles north of Harrisonburg, Rockingham County, Virginia. Same as locality 1 of Evitt and Whittington, 1953, p. 55. Collected and prepared by Dr. and Mrs. W. R. Evitt, Dr. G. Arthur Cooper, and Whittington.

Diacanthaspis cooperi Whittington, 1941

Locality 10 — Pasture on north side of Virginia secondary highway 772, about 1 mile east of Greenmount church, five miles north of Harrisonburg, Rockingham County, Virginia. Collected and prepared by Dr. and Mrs. W. R. Evitt.

Primaspis ascitus n. sp.
Diacanthaspis cooperi Whittington, 1941.

Locality 11 — Loose blocks in pasture on north side of Virginia secondary highway 616, ¼ mile east of intersection with Virginia secondary highway 699, and 2½ miles north-northeast of Spring Hill, 7 miles north of Staunton, Augusta County, Virginia. The Oranda formation immediately underlies the lower Martinsburg formation and outcrops a short distance to the west. The locality is that from which all the material described by me (including *Diacanthaspis cooperi*) in 1941 came. At that time (Whittington, 1941, p. 492) two localities were given, distant respectively 2½ miles north-northeast, and 3 miles north-northeast, of Spring

Hill and Long Glade. Spring Hill is a new name for the settlement formerly called Long Glade, and the confusion probably arose because the blocks of limestone were collected at different times (cf. Evitt, 1953, p. 34). The first blocks were collected by Dr. G. Arthur Cooper, later ones by Cooper and Whittington.

Locality 12 — In field on south side of Virginia secondary highway 753, 1 mile west of intersection with Virginia secondary highway 732, and 3½ miles north-northeast of Spring Hill, Augusta County, Virginia. This locality, visited by Dr. G. Arthur Cooper and Whittington, is one mile northeast of locality 11, and yields *Diacanthaspis cooperi*.

PART I: MORPHOLOGY, ONTOGENY AND EVOLUTION

Morphology of Holaspid Exoskeleton

The family diagnosis (p. 193) epitomises the morphology of an odontopleurid, and in this section certain aspects are commented on more fully, these being chiefly features on which I have information additional to that available to Prantl and Přibyl (1949).

Cephalon

Attitude: The characteristic attitude of the strongly convex cephalon is discussed below under "Mode of Life." The convexity of the cephalon and its position relative to the thorax and pygidium were recognized by some earlier authors (e.g. Weller, 1907, Pl. 23, figs. 1-4; Warburg, 1933, p. 9, footnote; see also Whittington and Evitt, 1954, p. 54), but not, apparently, by Barrande. Many of Barrande's drawings were made from specimens flattened in shale or calcareous mudstones, and show an exterior view of the cephalon combined with a dorsal view of thorax and pygidium (for definitions of these terms see Whittington and Evitt, 1954, p. 11). The present reconstructions attempt to remedy this situation (compare Text-figs. 4, 15, 25 with Barrande, 1852, Pl. 39, figs. 33, 1; Pl. 37, fig. 25, respectively).

Occipital ring: Conspicuous in odontopleurids is the way in

which the antero-lateral portion of the occipital ring merges with the inner posterior corner of the cheek. Behind this region the posterior border is distinctly separated from the remainder of the occipital ring, and the axial furrow more or less well developed, as it is beside the lateral glabellar lobes. The occipital ring in most odontopleurid genera is strongly convex and commonly elongated so that it projects behind adjacent parts of the posterior border. As Prantl and Přibyl pointed out (1949, p. 127), a median occipital tubercle is always present, and a median spine or paired spines may also be developed. The species of *Diacanthaspis* here described (Text-fig. 8) show that the median tubercle, or paired spines, or both may be greatly enlarged, or none may be especially prominent, in a group of closely related species. In genera such as *Ceratocephala* and *Miraspis* (Text-fig. 15), where long, stout, paired occipital spines are developed, a posterior occipital band, below and behind the bases of these spines, is developed (cf. Warburg, 1933). Such a band is, however, not present in *Acidaspis* (Text-fig. 13) or *Dicranurus* (Text-fig. 18), though the median (in the former) and paired (in the latter) occipital spines are large. The view of Reed (1925, p. 420) that the posterior occipital band represents the occipital ring, and that the part in front belongs to the glabella, has been adequately refuted by Warburg (1933) and Öpik (1937, pp. 45-47).

Where I have been able to observe both surfaces of the exoskeleton, as in *Primaspis ascitus*, n. sp. (Pl. 1, figs. 1, 6), the occipital lobes are small, gently convex, subcircular in outline, situated immediately behind the deep outer part of the occipital furrow. Their convexity, rather than any distinct furrow, separates them from the rest of the occipital ring inside and behind them, and they are indistinctly bounded posteriorly. On the inner surface they are seen to be in front of the outer part of the doublure of the occipital ring. In structure and position they are analagous to the lateral glabellar lobes, though they do not extend back to the posterior margin of the segment, and are much less distinct than the first and second glabellar lobes. In *Ceratocephala laciniata* and *C. triacanthcis* (Whittington and Evitt, 1954, Pl. 6, fig. 4; Pl. 8, figs. 1, 2; Pl. 25, figs. 10, 11) occipital lobes are scarcely distinguishable, whereas in certain

younger species of the same genus (e.g. Warburg, 1933, text-figs. 2, 3) the outer part of the occipital ring, between the occipital furrow and posterior band, is inflated. Similarly, in *Dicranurus hamatus* (Whittington, 1956b, Pl. 60, figs. 11, 12) the inflation of the antero-lateral part of the occipital ring, though vaguely defined, especially postero-laterally, is greater than in *D. monstrosus* (Text-fig. 18). Species of other genera show the same features, and indicate that, when occipital lobes are developed (they are absent altogether in some genera and absent in certain species only of other genera), they are situated in the antero-lateral corner of the occipital ring, probably outside the margin of the doublure, and ill-defined on the posterior and inner sides. Their variability suggests that presence or absence of such lobes can scarcely be used as a generic character.

Glabellar lobes and furrows: Two pairs of lateral glabellar lobes are always present, the first (basal) pair the larger, and, except in a few genera and certain species of other genera, small, variably-developed, third lateral lobes are present. Particularly in *Ceratocephala* and *Miraspis* the third lobes are small and depressed, and have been regarded as not developed by Prantl and Přibyl (1949, pp. 180, 194). The convexity of the lateral lobes and degree of their separation from the median glabellar lobe are variable (contrast, for example, *Leonaspis*, Text-figure 7, with *Whittingtonia*, Text-figure 17), and in *Apianurus* n.gen. and *Primaspis keyserlingi* (Barrande, 1852, Pl. 36, figs. 10, 12) the lateral lobes are fused. The peculiarities of the glabellar lobation of *Selenopeltis* (Text-fig. 25) set it apart. The frontal lobe varies in width, sometimes being only as wide as the median lobe (*Acidaspis*, Text-fig. 13) but usually it is expanded to extend in front of the second or third lobes (*Leonaspis* n. sp., Text-fig. 7; *Dicranurus hamatus,* Whittington, 1956b, Pl. 60, fig. 15; *Miraspis mira*, Text-fig. 15). The eye ridge terminates opposite the lateral extremity of the frontal lobe, and may merge into it (*Ceratocephala*, see Whittington and Evitt, 1954, Pl. 9, fig. 2) or be separated from it by a low depression, the axial furrow (*Primaspis ascitus* n. sp., Pl. 1, figs. 2, 5). Hupé's diagram (1953, p. 102, text-fig. 62; repeated in 1955, p. 236, text-fig. 205) conveys a misleading impression, in that figure 62 (1), showing 3 pairs of lateral glabellar lobes, is labelled "primitif"

and "normale," and figure 62 (3) with 2 pairs of lateral lobes, is labelled as showing "regression progressive et complète" of the fourth segment (from the posterior margin). In fact no such progressive reduction occurs, for genera with 2 and 3 pairs of lateral lobes appear at about the same time (*Diacanthaspis*, *Primaspis*, and *Ceratocephala*), and *Ceratocephala* and *Dicranurus*, both having 3 pairs of lateral lobes, are known in the Middle Devonian.

The outer part of the occipital furrow, and each glabellar furrow (especially at the inner end), is deepened and forms a strong ridge on the inner surface (Pl. 1, fig. 6; Pl. 5, fig. 4; Pl. 7, fig. 5; Pl. 12, fig. 7; Pl. 15, fig. 5; Pl. 20, fig. 11; Pl. 21, fig. 6; Pl. 22, fig. 6). The quartz along the crests of these ridges may appear darker, strengthening the impression that these ridges are points of muscle attachment. So far as is known, however, these thick ridges are not extended as ventral processes. The outer part of articulating and ring furrows is similarly deepened (e.g. Pl. 12, figs. 6, 18) but does not form so strong a ridge on the inner surface.

Eye lobe, eye ridge, facial sutures: The external covering of the eye of *Ceratocephala* has been described (Whittington and Evitt, 1954, p. 16) as having the outer surface smooth or faintly divided into numerous closely spaced, slightly raised facets, the inner surface showing shallow pits similarly arranged. The external covering of the eye of the silicified specimens of other genera described here appears to be similar, the facets on the outer surface sometimes clearly delineated (Pl. 2, figs. 18, 22; Pl. 3, fig. 21; Pl. 16, fig. 23; Pl. 17, fig. 21; Pl. 23, figs. 9, 10). This type of eye surface seems to be typical of odontopleurids.

The presence of the eye ridge, and of sutural ridges (Whittington and Evitt, 1954, pp. 13, 17-19), notably where the suture approaches either border, is characteristic.

Fusion of the facial sutures, presumably a secondary phenomenon, has been suggested as a criterion for distinguishing genera of odontopleurids. It is true that in some specimens in which the exoskeleton is preserved it is almost impossible to detect the course of the suture, but whether or not this means that secondary fusion has taken place is difficult to determine. In any event this single character is not regarded as a reliable

criterion upon which to base a genus (Whittington and Evitt, 1954, p. 53).

Librigenal spine: Prantl and Přibyl (1949, pp. 126, 131, etc.) stated that, in *Selenopeltis* and miraspinids, the librigenal spine arose from the "surface of the cheeks above the genal angle," rather than being a backward and outward extension of the rolled borders, at the genal angle, as it is in odontopleurinids. In *Ceratocephala* (Whittington and Evitt, 1954, Pl. 6, fig. 17; Pl. 25, figs. 12-14), the broad base of the librigenal spine merges into the upper surface of the posterior and lateral borders and the sutural ridge. In *Ceratocephala* (*Ceratocephalina* n. subgen.) (Pl. 16, figs. 23, 24) it likewise arises from the upper surface of the border, and a line of spines on the margin of the border is continuous below it. The fact that the doublure extends beneath the base of the librigenal spine (Pl. 16, fig. 9) shows that the spine arises from the border and not the surface of the cheek (cf. Whittington and Evitt, 1954, p. 52). Thus I do not agree with Prantl and Přibyl (1949, p. 131, etc.) that the miraspinid librigenal spine arises in a way that is fundamentally different from, and originates from other cephalic segments than, that of odontopleurinids. I believe rather that the difference between the librigenal spines in the two subfamilies is one of direction and not place of origin. In apianurinids the librigenal spine also arises from the cephalic border, but from a point farther forward. The ontogeny of *Diacanthaspis,* of *Apianurus* n. gen., and of *Ceratocephala* shows that the librigenal spine develops in much the same way in each group, but does not show to which cephalic segment it may belong.

Hypostome: The hypostomes of a species of *Primaspis* and those of *Apianurus* n. gen. and *Calipernurus* n. gen. are described here, and others in Whittington, 1956b. Thus the hypostomes of more than half of the odontopleurid genera are known, and seem to fall into four types, exemplified in Text-figure 2. The "family resemblance" between them is shown particularly by the small anterior wing (lacking the wing process), lateral notch and pointed shoulder, middle body with large depression in antero-lateral corner, from which the middle furrow runs inward and backward, and tiny posterior wing. The types distinguished form one of the main bases of the four subfamilies recognized.

Prantl and Přibyl (1949, p. 134, etc.) stressed the difference between the odontopleurinid and the *Selenopeltis-Ceratocephala* types of hypostome. The latter two present a considerable likeness, and in both the crescentic tip of the posterior lobe of the middle body is inflated and extends outside the depression in the antero-lateral corner of the middle body. In the odontopleurinid (and apianurinid) type the tip of the posterior lobe of the mid-

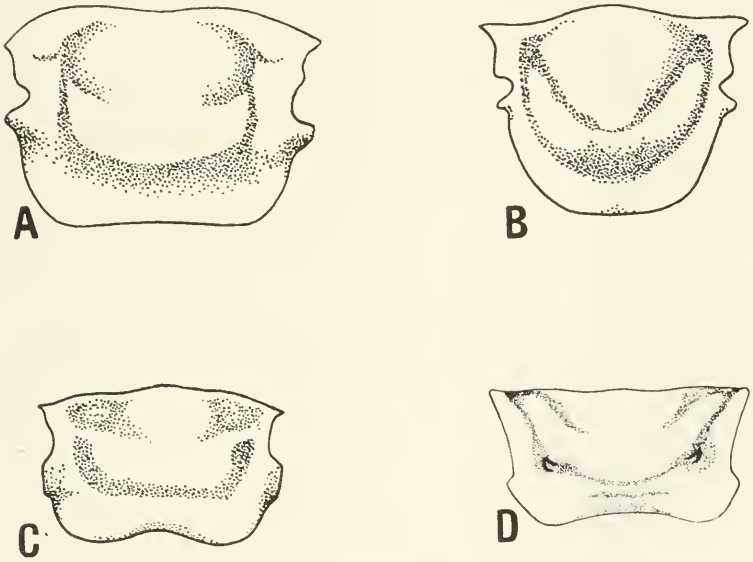


Figure 2. Hypostomes characteristic of each of the four subfamilies of Odontopleuridae. A, Odontopleurinae, *Primaspis*, based on that of *P. ascitus* n.sp. B, Apianurinae, *Apianurus*, based on that of *A. barbatus* n.gen., n.sp. C, Miraspinae, *Ceratocephala*, based on that of *C. laciniata* Whittington and Evitt. D, Selenopeltinae, *Selenopeltis*, based on that of *S. buchi* (Barrande).

dle body does not extend as far forward. I hardly think this difference is as great as Prantl and Přibyl tend to make it by saying that in odontopleurinids the middle furrow starts from the lateral border furrow, whereas in *Selenopeltis* and *Ceratocephala* it starts from the anterior border furrow.

The silicified specimens of hypostomes have shown the exist-

ence of a circular hole through the doublure (Pl. 3, figs. 9, 10; Pl. 10, figs. 21, 24; Pl. 13, figs. 9, 11; Pl. 14, fig. 12; Pl. 23, fig. 15), situated on or near the sharp flexure associated with the shoulder. This hole is seen in species belonging to several genera, but is not exhibited by all species of a single genus — for example, *Diacanthaspis*. A similar-appearing opening in the cephalic and thoracic doublure of other trilobites is the Panderian opening, but whether or not this similarity implies that they are analagous structures is uncertain.

The macula is not discernible in the odontopleurid hypostomes here studied, except perhaps as the smooth area at the inner end of the middle furrow of *Primaspis ascitus*, n. sp. (Pl. 1, fig. 20). The depression in the antero-lateral corner of the middle body is conspicuous, however, in that it is smooth on the external surface, and the quartz is often differently coloured, and on the inner surface there may be some exfoliation. Thus it resembles the similarly-situated area in *Sphaerexochus* (Whittington and Evitt, 1954, p. 25) and may be an area of muscle attachment.

The problem of the manner in which the hypostome is attached in odontopleurids has been discussed previously (Whittington, 1941, p. 516; Whittington and Evitt, 1954, pp. 20, 55-56). Isolated rostra of the silicified species have not been found, but the unique specimen of *Acidaspis cincinnaticnsis* recently described (Whittington, 1956b) has the rostrum in place. The posterior edge of this rostrum is straight (except distally where it curves to meet the inner edge of the cheek doublure), and obscurely bevelled in this specimen. Measurement shows that the straight edge fits exactly against the straight, bevelled, anterior edge of the hypostome. The fit of the bevelled edges suggests that the hypostome lies approximately in the horizontal plane (on the orientation adopted here), or slopes slightly downward and backward. The tip of the small anterior wing lies beneath the intersection of the axial and preglabellar furrows, just in front of the eye ridge. This intersection, and the border furrow just outside it, is usually deepened in odontopleurids, though it does not form a large projection on the inner surface. Thus the attachment of the hypostome seems to be as previously suggested — at the suture and with a muscular link between anterior wing and/or pit at anterolateral corner of the middle body to

unspecified point or points on cranidium. One of the latter is perhaps the preglabellar furrow and border furrow outside the inner end of the eye ridge (i.e. about where the anterior boss is in other trilobites). The hypostome of *Apianurus barbatus* n. gen., n. sp., is restored in approximately this position in Text-figure 20. This attachment appears not to have been as rigid as that in cheirurids and allied families (Whittington and Evitt, 1954, pp. 19-21), and the evidence cited by Prantl and Přibyl (1949, p. 196) of many specimens of *Miraspis mira* in which the hypostome is preserved but rotated through 180° and lying just in front of the cephalic margin, is interpreted by them as indicating an "easily movable connection." However, the flat surfaces that are apposed along the hypostomal suture are not suggestive of movement at the suture having been possible during life.

Antennular notch: Figures 5, 7, of Plate 17 show that there is a conspicuous notch in the anterior cephalic border immediately outside of where the connective suture crosses the border. It has previously been argued (Whittington and Evitt, 1954, p. 20) that the antennule is attached to the surface of the anterior boss and passes through the lateral hypostomal notch. It may also have passed through the notch (here called the antennular notch) in the anterior cephalic border, which would have permitted the antennule to be forwardly extended, when the cephalic margin was resting on the sea bottom, in the manner suggested under "Mode of Life." The antennular notch is developed to a greater or lesser extent in most odontopleurids (e.g. Pl. 1, figs. 2, 5; Pl. 12, fig. 2; Pl. 22, figs. 3, 6).

Thorax

The eight thoracic segments of *Leonaspis* n. sp. (Whittington, 1956b) are unusual, nine or ten being most commonly seen in the family. The backwardly-convex curve of the posterior margin of the prominent axial ring (and the occipital ring) is complemented by the curve of the articulating furrow. Medially, the ring adjacent to this furrow is less elevated. The articulating half ring is long (sag.), particularly that of the first segment. In some species and genera the antero-lateral part of the axial ring is inflated, e.g. *Selenopeltis* (Text-fig. 25), *Miraspis* (Text-

fig. 15), and *Proceratocephala* (Whittington, 1956b, Pl. 60, figs. 2, 10). A posterior band of the type seen on the occipital ring in some genera has not been seen on axial rings.

The horizontal pleurae may be unfurrowed as in *Apianurus* n. gen. (Pl. 18, figs. 6, 9) and *Ceratocephala* (Whittington and Evitt, 1954, Pl. 8, fig. 10), but are generally divided by the straight, transverse pleural furrow into a narrow anterior and wider (exs.) posterior band. The narrow, raised ridge of the posterior pleural band of *Selenopeltis,* with its strong curve convex forward, is distinctive. A posterior flange is present in many species. At the fulcrum the pleural bands are continued by spines: a stout, more or less horizontal, posterior spine, and one or more slimmer, shorter, anterior spines, downwardly directed. The doublure is curled under at the base of these spines, and forms the fulcral articulating socket and process. In odontopleurinid genera the broad-based librigenal spine is directed horizontally outward and backward beside the thorax, and consequently the first two or three thoracic pleurae are facetted so that they fit beneath the posterior cephalic border and librigenal spine. Thus the anterior pleural spine is absent, and the posterior pleural spine short (e.g. Pl. 3, fig. 11; Pl. 8, fig. 12). The anterior pleural spines of the third or fourth, and successive, segments are present and the posterior pleural spine is long and backwardly directed. In miraspinids (Text-figs. 15, 18) and apianurinids (Text-fig. 19), however, the librigenal spines are respectively directed upwardly, and situated far forward on the cephalon, and no facetting and truncation of the thoracic pleural terminations is necessary to permit fitting behind the cephalon. Thus the posterior pleural spines are successively directed obliquely forward, outward, and obliquely backward. This difference in development and direction of pleural spines has been regarded by Prantl and Přibyl (1949) as indicating a distinction of family rank between odontopleurinids and miraspinids, but hardly seems to be of this magnitude (cf. Whittington and Evitt, 1954, p. 52). Likewise the "stunting" of the first two or three thoracic segments hardly seems an adequate basis for the subgenus *Leonaspis* (*Kettneraspis*) Prantl and Přibyl (1949, p. 165; see Whittington, 1956b).

An inflation of the posterior pleural band at the fulcrum

characterises certain odontopleurinids, e.g. *Primaspis* (Pl. 1, figs. 11-14), some species of *Leonaspis*, and *Acidaspis* (Whittington, 1956b) and may indicate relationship.

Pygidium

Major border spines, i.e. one notably larger pair among the several arising from the pleural regions, are characteristic, but may not be developed at all (*Diacanthaspis secretus* n.sp., Pl. 7, fig. 10; *Radiaspis radiata*, see R. and E. Richter, 1917, text-fig. 10) or only slightly developed, as in some species of *Ceratocephala* (Barrande, 1852, Pl. 38, figs. 5, 18). When present, the major spine is connected at its base to the first axial ring by the pleural ridge which runs across the pleural region. Commonly, the major spine arises from the upper surface of the pygidial border, but may take its origin from inside the border of the pleural region (e.g. *Diacanthaspis orandensis* n.sp., Pl. 10, figs. 17-19; *Apianurus barbatus* n.gen., n.sp., Pl. 18, fig. 12; *Calipernurus insolitus* n.gen., n.sp., Pl. 24, figs 27, 28). In this latter case it seems quite independent of the border spines, though the pleural ridge is present. When the major spine arises from the border it is commonly the third or fourth spine, and in *Miraspis* is unusually far forward on the border, though still the third spine (cf. Prantl and Přibyl, 1949, pp. 128-129). As remarked under "Locus of segmental divisions" the major spine and pleural ridge are homologous with the thoracic posterior pleural band and spine.

The doublure of the pygidium is curled under, not wide, and there is a small projection posteriorly, directed up toward the axis.

External Surface

Short, thorn-like spines, tubercles, and granules are characteristic; their form and arrangement are shown by the plates (cf. Whittington and Evitt, 1954, Pls. 6-9, 25, 26). Rarely is the external surface everywhere smooth, as it seems to be in *Primaspis keyserlingi*, but commonly the deeper parts of furrows, and the doublure, are smooth. A symmetrical arrangement of the prominent spines, making transverse rows across the exoskeleton,

is typical of early developmental stages (see below) and may persist into the adult. In most adults this symmetry is less obvious, and may be lost altogether (e.g. *Primaspis ascitus*, Pl. 1, fig. 1). Conspicuous paired spines on axial rings are common, though rarely are they as large on the thoracic rings as in *Proceratocephala* (Whittington, 1956b, Pl. 60, figs. 2, 5, 10).

It was shown previously (Whittington and Evitt, 1954, pp. 56-59, text-fig. 1, etc.) that small openings occur on the distal side of tubercles scattered along occipital and librigenal spines, and at and near the tips of spines on the cephalic and pygidial border. Such openings are characteristic of the specimens described here (e.g. Pl. 7, figs. 12-14; Pl. 11, fig. 16; Pl. 13, fig. 14; Pl. 23, fig. 6; Pl. 24, figs. 21, 24). It was further suggested that in *Ceratocephala laciniata* there may have been a single opening, possibly occupied by a hair, at the tip of the thorn-like spines (Whittington and Evitt, 1954, p. 59; Pl. 8, fig. 11; Pl. 9, figs. 2, 4; text-fig. 1) scattered over the external surface of the cranidium. Among the few available cranidia of *C. rarispina* n.sp., however, is one (Pl. 15, fig. 28) in which the thorn-like spines, where not obviously broken, are closed at the truncated tip by a plate in which there are minute depressions (appearing as dark spots in the photograph). The diameter of these depressions is less than that of some of the quartz grains replacing the exoskeleton, so that it is difficult to be sure of their nature. It seems probable that they are the orifices of canals through the exoskeleton. The thorn-like spines on the cranidium of *Diacanthaspis* are similar, sometimes showing an evenly cut off tip with a relatively large central opening (Pl. 7, fig. 15). A well-preserved specimen of *D. scitulus* n.sp. (Pl. 13, figs. 16, 17), however, has the truncated tip covered by a convex plate in which there are tiny depressions. These may show a regular arrangement of a central larger pit surrounded by smaller pits. A specimen of *D. lepidus* n.sp. (Pl. 4, fig. 22) shows a similar arrangement. In *D. cooperi* and *D. orandensis* n.sp. (Pl. 9, fig. 6; Pl. 11, fig. 19) the tip is slightly expanded and subspherical, with a large central depression or opening surrounded by smaller ones. In *D.* aff. *ulrichi* n.sp. (Pl. 9, figs. 7, 9) some spines show only a central opening, and others appear to show several openings. One may conclude that in *Diacanthaspis*, as in *C. rarispina* n.sp.,

the tip of the thorn-like spines was pierced by one or more minute openings, but whether a hair issued from each opening is uncertain. The tubercles of *Primaspis ascitus* n.sp. (Pl. 2, fig. 21) appear to be closed at the summit, and in *Apianurus barbatus* n.gen., n.sp. (Pl. 18, figs. 19, 22) the characteristically curved tips of the thorn-like spines appear closed.

In *Diacanthaspis lepidus* n.sp. (Pl. 5, fig. 1), *D. secretus* n.sp. (Pl. 6, fig. 22), and *D. ulrichi* n.sp. (Pl. 8, fig. 27) the tip of the librigenal spine is hooked. The hooked portion appears to be smooth, without openings, but proximally to the tip the usual type of opening is present. Such openings are numerous at the tip of the librigenal spines in species which do not have the hook (Pl. 13, fig. 14).

Tubercles on the external surface, as in *Primaspis ascitus* n.sp. or *Calipernurus insolitus* n.gen., n.sp., seem never to have had openings at the summit. The median occipital tubercle in both these species, however (Pl. 2, figs. 21, 23; Pl. 23, figs. 5, 7, 8), is larger than any other, and has four pits, arranged to outline a square (and rarely a faint, small, median pit) in its low, domed surface. It appears early in ontogeny (Pl. 2, figs. 6, 8; Pl. 24, fig. 1) and is retained in the largest holaspis known. The pits, appearing as dark spots, do not seem to be the openings of canals through the exoskeleton. The occipital doublure extends close underneath the tubercle and well in front of it in *P. ascitus* n.sp. (Pl. 1, fig. 6). No similar tubercle is seen on the axial rings of thorax or pygidium. The same type of median occipital tubercle has been observed in other species of *Primaspis*, in *Diacanthaspis cooperi* (Pl. 11, fig. 18), *D. ulrichi* n.sp. (Pl. 8, figs. 24, 30), *D.* aff. *ulrichi* n.sp. (Pl. 9, figs. 8, 9), *D. orandensis* n.sp. (Pl. 11, fig. 20), and *Leonaspis leonhardi* Barrande. This tubercle may be compared with the median glabellar tubercle of *Tretaspis seticornis* (Stormer, 1930, pp. 85-87, figs. 36, 37), which is similar but displays more clearly a fifth, centrally situated pit, as does the four-celled sense-organ of *Anaspides* (Hanström, 1934). Temple (1952, pp. 254, 258) has described the median occipital tubercle of protaspid and early meraspid stages of *Dalmanitina olini* as bearing five tiny tubercles, one central and the others forming a square. This may be an anala-

gous organ to that of the odontopleurids, but represented by tubercles rather than pits.

Hupé (1953, pp. 80-81) suggests that the median glabellar tubercle is the specialized homologue of median tubercles of succeeding segments, and this example in odontopleurids may represent such a specialization (presumably for some sensory function) of the median occipital tubercle.

Abnormal Specimens

Parts of exoskeletons showing marked deviation from the normal structure are rare, as they also seem to be in other collections of this type (cf. Ross, 1951, p. 134). The only examples among the present material are the single free cheek of *D. scitulus* n.sp. (Pl. 13, figs. 6, 7; the emargination apparently resulting from an injury) and the three pygidia of *Calipernurus insolitus* n.gen., n.sp. (Pl. 24, figs. 11, 17, 18, 20). As compared to the usual form (Pl. 24, fig. 27), these pygidia either lack one of the three posterior border spines, or have a single spine which bifurcates distally. This appears to be the result of abnormal growth rather than injury, and another specimen (Pl. 24, fig. 28) shows that even when three border spines are present, they may be markedly unequal in size. Abnormal specimens of the pygidium of *C. insolitus* n.gen., n.sp. form some 15 per cent of the total known, as compared to one injured free cheek of *D. scitulus* n.sp. in 38 specimens.

Ontogeny

It has been shown elsewhere (Whittington, 1956a) that the supposed odontopleurid protaspis described by Beecher is a phacopid. Whittington and Evitt (1954, pp. 28-31) described the meraspid and later ontogeny of two species of *Ceratocephala*, and made general observations on odontopleurid ontogeny. This section supplements the earlier account. Here odontopleurid protaspides are described for the first time, the three best-known examples (Pl. 3, figs. 1, 2; Pl. 4, figs. 1-5; Pl. 6, figs. 1-5; Text-figs. 9, 11) being different species of *Diacanthaspis*. Most remarkable is the presence of fixigenal spines. The spines on the dorsal surface are relatively large and arranged in a symmetri-

cal pattern (numbered and lettered here as in Text-fig. 1), there being a median occipital, three pairs on the glabella (2-4), and a pair on the anterior border just in front of 4 and slightly farther apart. On the glabella the occipital furrow is shallow, and in *D. cooperi* and *D. lepidus* n.sp. the basal glabellar lobe is faintly delineated. The eye lobe is situated near the antero-lateral border of the cheek, the two branches of the suture aligned and isolating a narrow (tr.) free cheek, which bears a row of border spines, the posterior the longer. The posterior branch of the suture cuts the margin immediately outside the fixigenal spine. A rostrum is present and the hypostome relatively large. The succeeding Stage 0 of each of these three metaprotaspides is known (Text-figs. 9C, 11B; Pl. 4, fig. 6) as is Stage 0 of *Apianurus barbatus* n.gen., n.sp. (Text-fig. 22A). Fixigenal spines persist, but long, stout librigenal spines are also present in species of both genera. Some additional spines (including axial 5 in *A. barbatus*) appear on the dorsal surface.

In the next largest specimens known of *Diacanthaspis* (Text-figs. 9D, 11C) and *Apianurus* (Text-fig. 22B), specimens which must represent the exoskeleton at Stage 1, the stout fixigenal spine has disappeared. There is no trace of where it has been, unless it is represented in *Apianurus*, greatly reduced, by one of the tiny spines between B and C on the extremity of the posterior border (Text-fig. 22B). However, there are tiny spines in this position in the smaller cranidia between B and the fixigenal (Text-fig. 22A), and most probably these are the spines seen at the extremity of the posterior border in the next stage. One or two specimens (Pl. 19, figs. 4, 6) of *Apianurus* have the fixigenal on one side and not on the other. It is hard to know whether this is the result of accidental breakage (and the fragility of the specimen at the base of the spine makes this likely), or whether it is showing the abrupt loss of the fixigenal on one side before the other. The course of the posterior branch of the suture is a curve across the ventral side of the base of the fixigenal spine. After the fixigenal is lost, the curve is similar, but runs across where the dorsal side of the base would have been. Thus little modification of the course of the posterior branch of the suture, and of free cheek outline, is caused by the loss.

In *Diacanthaspis*, spines A_1, B, C, D, and the fixigenal are

present on the postero-lateral part of the fixed cheek of the protaspis and Stage 0 cranidia. In the next largest size the fixigenal is gone and A_1, B, C, and D remain. The free cheek shows no sudden modification as the fixigenal is lost — the eye lobe moves back and the course of the sutural branch is altered slightly accordingly (Text-fig. 9D).

Thus the cephalon of *Diacanthaspis,* and of *Apianurus,* is, at about Stage 1, "opisthoparian." Evidently the change takes place rapidly, for there is little difference in size between cranidia with and without the fixigenal spine (e.g. Pl. 6, figs. 6, 8; Pl. 19, figs. 2, 4, 9). If the loss is by reduction, as it is in such genera as *Sphaerexochus* (Whittington and Evitt, 1954, Pls. 17 and 32) or *Flexicalymene* (Whittington, 1941, Pl. 72), then this reduction is a far less gradual process in odontopleurids. No transitional specimens showing such a gradual reduction have been found, however, and the evidence points to the process being one of abrupt loss taking place, perhaps between moults, in the transition from Stage 0 to Stage 1.

The Stage 0 exoskeletons of *Diacanthaspis* and *Apianurus,* genera placed in separate subfamilies, are so similar that we may reasonably expect other odontopleurid protaspides to be like those of *Diacanthaspis* — gently convex; fixigenal spine like the two on border of protopygidium; free cheek narrow (tr.), bearing a librigenal spine; eye lobe far forward on the antero-lateral slope; glabella parallel-sided, divided by the occipital furrow, in front of which there may be small, low, basal lobes, and bearing a median occipital and, if any axial spines, numbers 2, 3, 4, and perhaps 5; fixed cheeks bearing some or all of the spines lettered in Text-figure 1. The Stage 0 cranidium of *D. ulrichi* (Text-fig. 12A) shows how smooth the external surface may be, compared to that of *D. lepidus* or *D. secretus.*

The meraspid development of the different genera also proceeds along parallel lines — as has already been observed in species of *Ceratocephala* and *Diacanthaspis* (Whittington and Evitt, 1954, pp. 28-31). In *Diacanthaspis cooperi* and *D. lepidus* n.sp., small, low, basal lateral glabellar lobes are present in the metaprotaspis at the base of the gently inflated fronto-median glabellar lobe, and the axial furrows are broad and shallow. The second lateral lobes appear later, after Stage 0. In *D. secretus*

the basal glabellar lobes are not apparent until after Stage 0, but this may be because they are obscured by the large spines on the external surface. In *Ceratocephala* the fronto-median glabellar lobe is strongly convex in the earliest known stages (Text-fig. 16), standing high above the broad axial furrows. At the next known stage (Pl. 14, fig. 2) basal glabellar lobes appear in the trough of the axial furrows. Thus, as pointed out previously (Whittington and Evitt, 1954, p. 29), the strongly convex axial region of the tiny *Ceratocephala* cranidium is homologous with the fronto-median lobe only of later stages, and the true boundaries of the glabella lie somewhere just outside, in the axial furrow. In the protaspis of *Diacanthaspis* the second segment (axial 2) is the longest (sag.), and axial 5 unmarked. In early meraspid stages of *Ceratocephala* (Whittington and Evitt, 1954, fig. 16; 2a is labelled "2"), *Apianurus* (Text-fig. 22B), and some species of *Diacanthaspis* (e.g. Text-fig. 9D), axial 2 is conspicuously longer and axial 2a is present. Axial 3 and 4 are progressively shorter, and 5 (which appears in *Apianurus* at Stage 0 but later in some species of *Diacanthaspis*), is the shortest. Subsequent growth of the glabella continues this trend, the second segment expanding and lengthening, the third likewise, but to a lesser extent, and the fourth and fifth remaining short. Neither 4 nor 5 disappears completely, and it seems unlikely that 4 disappears in *Leonaspis*, as implied by Hupé (1953, p. 102, fig. 62 (3)).

In the odontopleurid protaspis, as in those of, for example, cheirurids, phacopids, calymenids, and pliomerids, the eye lobe is situated inside the margin of the cheek, a short way up the antero-lateral slope. The facial suture is completely developed and is not marginal, and, in the late metaprotaspis (if not before), rostral, connective, and hypostomal sutures are present. The backward migration of the eye during ontogeny occurs in all odontopleurids, and is most marked in odontopleurinids and apianurinids.

A characteristic feature of odontopleurids is the way in which the antero-lateral extremity of the occipital ring merges into the inner corner of the cheek, and thus the posterior border is widest (exs.) distally, narrowing proximally to disappear at the axial furrow. At Stage 0 in *Diacanthaspis cooperi* (Text-fig.

9C), and in slightly later stages of other species of *Diacanthaspis* (Text-fig. 11C, 11D), in *Ceratocephala* (Text-fig. 16), and in *Apianurus* (Text-fig. 22C), there is a spine (A_1) in the inner corner of the free cheek where it passes into the occipital ring, and the posterior border widens (exs.) rapidly outwards. In later stages inflation of the inner corner of the fixed cheek accompanies the expansion of the posterior part of the glabella and backward movement of the eye lobe.

The border spines of the protopygidium and early transitory pygidium of *Diacanthaspis*, and of the early transitory pygidium of *Apianurus*, become respectively posterior pleural, and pleural, spines of the thorax. Anterior pleural spines are tiny and appear low down on the edge of later transitory pygidia of *Diacanthaspis* (Pl. 3, fig. 18), but never appear in *Apianurus*. The earliest known transitory pygidia of *Ceratocephala* (Whittington and Evitt, 1954, Pl. 8, fig. 4; Pl. 26, fig. 1) have the two types of border spines, those corresponding to the posterior pleural being relatively larger, as they are in the thorax.

Attention has been drawn to the likenesses between early developmental stages of different odontopleurid genera, i.e. to the generalized family characters appearing first in ontogeny. Although the later developmental stages follow a somewhat parallel course, it is also true that out of the general characters the more special characters are developed, so that during ontogeny each species diverges more and more from all others as it takes on its distinctive holaspid form. No better example of von Baer's "laws" could be wished for (cf. de Beer, 1951, pp. 2-3). At Stage 0 we can clearly recognize not only family but generic characters, and the ontogenies of the species of *Diacanthaspis* suggest that specific characters are recognizable at this stage, and probably still earlier, in the metaprotaspis. Thus, in the earliest known ontogenetic stages, while general characters are most obvious, special characters are expressed in the details of morphology. Could we go farther back in ontogeny, into the anaprotaspid stages and embryonic stages, we might find those points at which only higher systematic categories — superfamily, order, or even class — are recognizable.

Locus of Segmental Divisions

The occurrence of axial spine pairs, and of transverse, sym-

metrical spine-rows in the protaspides and Stage 0 specimens of odontopleurids is emphasized by the new evidence given here (Text-figs. 9, 11, 22), and is manifestly a fundamental character. On the cephalon (Text-fig. 1), spines A_1, B, and C form a row with axial spines 1, A_2 and D with axial 2, A_3 with axial 3, Er and Pl with axial 5. These rows seem without much doubt to reflect segmentation, and the fixigenal spine, with B at its base, belongs to the posterior row. Each of the two or three border spines of the protopygidium has an upwardly-directed spine at its base (Pl. 3, figs. 1, 3; Pl. 4, figs. 1, 4; Pl. 6, figs. 1, 5, 10; Pl. 19, fig. 5), and the homology with the fixigenal and spine B is clear. These border spines of the protopygidium will become successive posterior pleural spines of the thorax. Thus there seems no reason to doubt that the joint between cephalon and protopygidium corresponds with a primary segmental division in the animal, as do the joints between successive thoracic segments, and that the fixigenal and posterior pleural spines are homologous.

The holaspid exoskeleton affords evidence in support of this interpretation, and three examples may be offered:—

1) *Primaspis ascitus* (Pl. 1, figs. 1, 11, 14). Posterior, most convex part of occipital ring, curving forward distally to occipital lobe, parallels structure and ornament of thoracic axial ring; posterior border is narrow (exs.) and smooth proximally, widened and inflated distally and tuberculate, as is the posterior band of the thoracic pleura; posterior border furrow is like pleural furrow; anterior band of pleura must correspond to most posterior part of cheek.

2) *Diacanthaspis ulrichi* n.sp. (Pl. 8, figs. 1, 12, 13, 21, 24) affords corresponding evidence, the spines on occipital and thoracic ring, and on posterior border and posterior band, being similar in size and arrangement.

3) *Calipernurus insolitus* n.gen., n.sp. (Pl. 23, figs. 3, 5, 7; Pl. 24, fig. 16). The highest, median part of the posterior border and lateral part of the occipital ring form a conspicuous smooth band, which seems to pass behind the paired occipital spines, and distally ends a short distance inside the suture. On the thoracic segment the smooth band runs along the highest part of the axial ring and pleural ridge.

Many other examples could be used, and it is notable that, in some, one could readily assume that the librigenal and posterior pleural spines were corresponding structures. This does not appear likely, however, in the apianurinids, and early ontogenetic stages of odontopleurinids seem to preclude this view and to show that the librigenal spine belongs to some segment in front of the occipital.

Study of the pygidium of *P. ascitus* n.sp. (Pl. 1, fig. 9) and of *D. ulrichi* n.sp. (Pl. 8, fig. 6) shows how like the posterior band and posterior pleural spine is the pleural ridge and major border spine. The Stage 8 transitory pygidium of *D. cooperi* (Pl. 3, figs. 17, 18) brings out strongly this likeness, and I have little doubt but that pleural ridge and major border spine of pygidium are homologous with posterior pleural band and spine. This means that the anterior 2 or 3 pairs of border spines are homologous with the anterior pleural spine, and their number is added to during ontogeny. For example, in *Apianurus barbatus* n.gen., n.sp., a small holaspid pygidium (Pl. 18, fig. 18) has one border spine in front of the ridge bearing the major spine, a larger holaspid has two (Pl. 18, fig. 12).

The similarity in structure between occipital ring, posterior border, and adjacent part of cheek and axial ring and pleura of thorax in odontopleurids has been noted before (Warburg, 1933). These trilobites afford no support for the view of Størmer (1942, p. 130) that "the transverse joint between the pleurae of the thoracic segments, or between these and the cephalon or pygidium, are secondary formations crossing the primary segments." Størmer based his argument mainly on an interpretation of *Holmia* and *Paradoxides*, and believed that in these trilobites each thoracic pleural spine belonged to the axial part of the segment in front of it (Størmer, 1942, text-figs. 14, 15a, 15c). In *Selenopeltis* (his text-fig. 15b) he represented the possible secondary segmentation as different in character, for each thoracic pleural spine belonged to the segment it was attached to, the "secondary segmentation" only affecting part of the pleura. There seems no evidence in odontopleurids for such a secondary joint, but in any genus other than *Selenopeltis*, which has the peculiar forward bend of the posterior pleural ridge, it would be hard to detect. Hupé (1953, pp. 118-119) does not support Størmer's suggestion.

Mode of Life

The spininess of the exoskeleton and the wide and seemingly rapid geographical distribution (many genera make their appearance almost simultaneously in two continents — Prantl and Přibyl, 1949, pp. 209-212) of many genera have led most students to regard odontopleurids as floating in habit (e.g. Prantl and Přibyl, 1949, pp. 132, 209; Whittington and Evitt, 1954, pp. 32-33, and references). The present study provides additional evidence for the view elsewhere expressed (Whittington, 1956b) that the convex cephalon will rest on a level surface on the anterior and lateral margins of the cephalon, the occipital ring the highest region, the posterior margin approximately vertical. In this position the thorax and pygidium, when stretched out horizontally, lie a short distance above the level surface. The outer surface of the hypostome lies roughly parallel to this surface and must be close to it. Antennular notches are commonly developed in the anterior cephalic margin, presumably so that the antennae may protrude forward while the animal rests on the cephalic margin. The cephalon is "propped" in this characteristic attitude by the development of either of two structures, or a combination of them. These are: (1) expansion of the lateral areas of the cheek, as in *Ceratocephala* (Whittington and Evitt, 1954, fig. 14), *Selenopeltis* and *Dicranurus* (Text-fig. 18); (2) development of a fringe of spines on the lateral cephalic border, increasing in length posteriorly, as in *Acidaspis*, *Dudleyaspis*, *Miraspis*, and *Diacanthaspis* (Text-figs. 10, 13-15). A combination of the two structures is seen in *Whittingtonia* (Text-fig. 17), and in *Apianurus* (Text-fig. 19) the basal parts of the librigenal spines act as "props." The possibility of resting in this position being universal among odontopleurids, and its attainment by the development of a variety of structures, attests that it was of fundamental importance, and that odontopleurids commonly rested in this attitude. It may well have been a feeding position on the sea bottom, movements of the appendages causing food-carrying currents to move forward under the head toward the mouth. This position — resting on the cephalic margins and with the thorax and pygidium stretched out above the bottom — is characteristic of diverse trilobites, such as Harpidae (Whittington, 1950, pp. 25-26), Bathyuridae (Whit-

tington, 1953, p. 651, Text-fig. 1), and some illaenids and cheirurids. It seems, therefore, that while the spinose exoskeleton probably aided the animal in floating, and may have had a protective function, other features point to the odontopleurid as having rested on the sea bottom for at least part of the time. We need not necessarily regard odontopleurids as entirely pelagic, then, but rather as drifting (and feebly swimming?) at some depth in shallow seas, and resting at times on the bottom. Odontopleurids occur in limestones ranging from light-coloured, coarsely crystalline to dark, aphanitic, muddy and silty, and in a variety of mudstones, shales, siltstones and fine sandstones. They seem to have been preserved in a wide variety of shallow water marine environments, and particular genera, and sometimes species, occur in a variety of rock types. This mode of occurrence might be used as an argument for their being mainly or wholly pelagic. The wide geographical distribution, however, does not necessarily imply a pelagic mode of life, for the early developmental stages were floating and would permit this wide distribution. It is notable that, in the development of *Diacanthaspis cooperi* (Text-fig. 9), the lateral cephalic spines develop rapidly in the earliest meraspid stages, after the fixigenal spines are lost. It may be at about this stage that the change from entirely floating to a partially bottom-dwelling mode of life occurs.

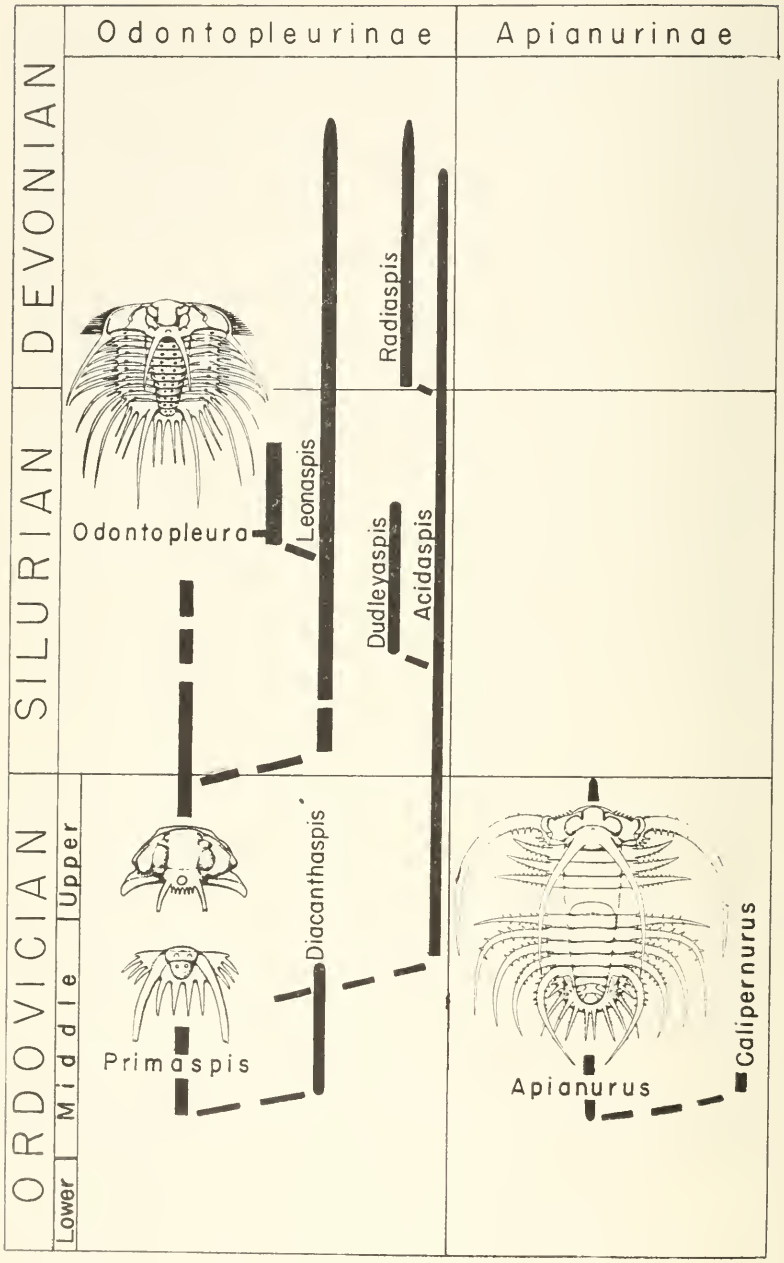
Origin and Evolution

Text-figure 3 summarizes my views on the taxonomy and evolution of the Odontopleuridae, and reasons for this arrangement are given in the systematic section. The earliest representatives of the family appear to be recorded from the Arenig (Canadian) — *Selenopeltis* in Shropshire, England (Whittard, 1952, p. 158), and pygidia of odontopleurinid type from Öland, Sweden (Bohlin, 1949, pp. 539, 560, 566). A pygidium of the latter type was described by Öpik (1926) as *Acidaspis solis,* and came from beds of early Llanvirn age in Estonia. The cranidium described by Hintze (1953, Pl. 19, fig. 16) is of about the same age — late Canadian or immediately post-Canadian, and by this time *Selenopeltis* is widespread in western Europe and North Africa. By late Llandeilo time other genera have appeared — *Primaspis*

in Bohemia and *Ceratocephala* and *Apianurus* n.gen. in the Lincolnshire limestone of Virginia. Thus in a relatively short span of time odontopleurids appeared and diversified into the types here regarded as constituting four subfamilies. These early genera are at present known from widely separated geographical areas, and correlation between the rocks containing them, and thus relative times of appearance, can be only generalized. Thus one cannot with any confidence single out the earliest stock or a geographical area in which odontopleurids arose and from whence they spread out. Prantl and Přibyl (1949, p. 212) pointed to the Upper Ordovician of Scotland as the time and region where the first differentiation of odontopleurids took place, but this evidently is not so. Comparative morphology seems to throw no light on origins either, for other Canadian trilobites seem not to be closely related. The peculiarities of the odontopleurid protaspis serve to emphasize the lack of obvious relationship between the family and its contemporaries. In seeking the ancestors of the Odontopleuridae, "The possibility that groups hitherto soft-shelled were acquiring the power to mineralize the exoskeleton cannot be overlooked" (Whittington, 1954, p. 198; cf. Rasetti, 1948, p. 5). Yet as Professor R. Kozlowski has pointed out to me (personal communication), the sudden appearance of new types is a frequent phenomenon in the history of this and other animal groups, and alternative explanations can be offered for these appearances.

The initial diversification of the odontopleurids established the four subfamily types, illustrated in Text-figure 3 by *Primaspis*, *Ceratocephala*, *Apianurus* n.gen., and *Selenopeltis*. Though these

Figure 3. Classification, relationships and range in time of the genera of the Odontopleuridae. Characteristic members of each subfamily are shown, reproduced from Figures 4, 5, 19A, and 25C. *Ceratocephala* from Whittington and Evitt, 1954, figure 13. Range of each genus shown by solid black bar, bar broken if range uncertain. Broken diagonal lines suggest relationships between genera. Numbers of genera through time proportional to width of bar at right. Lower, Middle, and Upper divisions of the Ordovician correspond with the three Ordovician Series of Twenhofel et al., 1954.


Odontopleurinae
Apianurinae
ORDOVICIAN
SILURIAN
DEVONIAN
Lower
Middle
Upper
Odontopleura
Leonaspis
Radiaspis
Dudleyaspis
Acidaspis
Diacanthaspis
Primaspis
Apianurus
Calipernurus

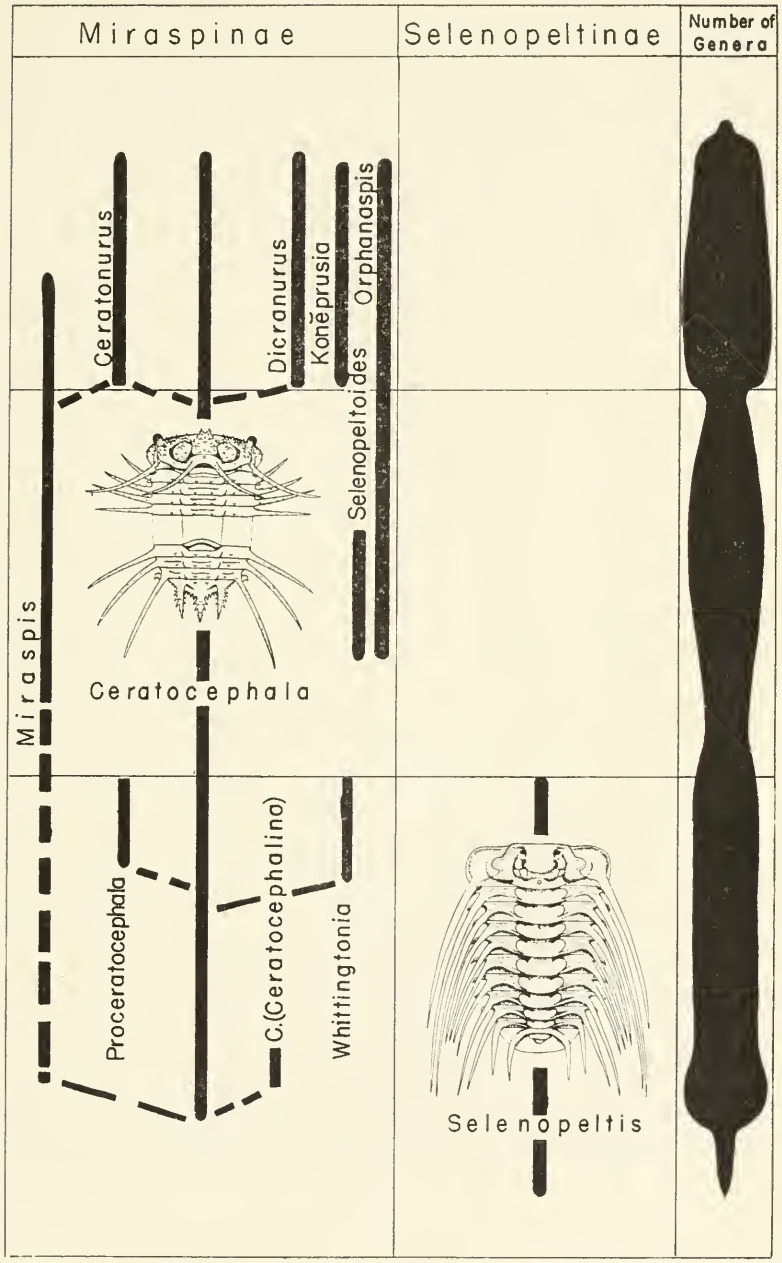

Miraspinae
Selenopeltinae
Number of Genera
Ceratonurus
Dicranurus
Konĕprusia
Orphanaspis
Selenopeltoides
Miraspis
Ceratocephala
Proceratocephala
C.(Ceratocephalina)
Whittingtonia
Selenopeltis

Figure 3

four groups have much in common, each has its distinctive characters, one of the most important being the type of hypostome (Text-fig. 2). There is no comparable diversification after this, for only two subfamilies survive the Ordovician and no new ones arise. In later Middle Ordovician times three (and possibly a fourth) new genera and one new subgenus arise (making a total of at least eight in the Middle Ordovician), and two new ones appear in Upper Ordovician times. During the Silurian period five new genera arise, and in the Devonian four. In the Middle and earliest Upper Devonian the nine surviving genera become extinct, this extinction being almost as rapid as the early diversification. Text-figure 3 shows the variation in time of number of genera and reflects the abrupt appearance and extinction of the group, though not the maximum morphological diversity of Ordovician time. A striking feature of odontopleurid evolution is the long range in time of certain genera — *Ceratocephala* endures for some 100 million years, and each of four other genera, *Primaspis, Leonaspis, Acidaspis* and *Miraspis,* for some 50-70 million years (on present estimates of absolute time). Other genera appear to have a relatively much shorter range. It is suggested here (Text-fig. 3) that certain of these long-ranging genera provided a root-stock from which the short-ranging genera were derived. *Ceratocephala* affords the best example, the other miraspinid genera differing from it in one or more morphological characters (e.g. the big paired occipital spines of *Dicranurus,* or the inflated median glabellar lobe of *Whittingtonia*) but retaining the main structural plan. Not all the seemingly derived genera are short-ranging, e.g. *Miraspis,* though this genus may prove to be rather a closely related but distinct root-stock. *Acidaspis* and *Primaspis-Leonaspis* seem to be the root-stocks of the Odontopleurinae. The other two subfamilies are relatively short-lived, not so diverse, and the Selenopeltinae especially seem an aberrant off-shoot.

If any general picture is afforded by the pattern of odontopleurid evolution, it seems to be one of persistent main themes and relatively brief appearances of variations on these themes. Some of these variations, such as large, paired or single, occipital spines, major pygidial spines, marked inflation of certain glabellar lobes, appear more than once during the history of the family, and in different combinations, suggesting a process of shuffling

of morphological characters.

The stratigraphical position of each of the species of *Diacanthaspis* is shown in Text-figure 8. There appear to be three main strands within the evolving plexus of species, viz. *orandensis-cooperi*, *lepidus-secretus-scitulus*, and *ulrichi*-aff. *ulrichi*. The species are similar to each other, the distinctions being size and length of median and/or paired occipital spines, outline of glabella and degree of inflation of lobes, presence or absence of, and position of origin of, major pygidial spine, size and distribution of spines on external surface, etc. The illustrations show that these characters are relatively minor distinctions within a major framework, and that they appear and disappear, forming different combinations. Thus the species of *Diacanthaspis* show the same evolutionary pattern in a part of the family as in the whole—the presence of several main themes, occurrence of minor variations on these themes, and shuffling and recombinations of characters within the plexus. No other genus is represented in the collections by as many species as is *Diacanthaspis*. In other genera represented by more than one species no particular trends of morphological change are evident.

Turning to consider the rate of morphological change among the silicified trilobites, it is seen to be variable in different lines during lower Edinburg to Oranda time—*Apianurus barbatus* n.gen., n.sp., shows no change, and there is little in the *Diacanthaspis ulrichi*—aff. *ulrichi* line, while the *D. lepidus-secretus-scitulus* line shows considerably more. *Ceratocephala* is present in the pre-Edinburg Lincolnshire limestone (*C. triacanthcis* Whittington and Evitt, 1954), a second species *C. laciniata* is common in the lower Edinburg, and *C. rarispina* n.sp. is rare in the Oranda. Thus there is change in this presumed line of descent, though no particular trend is evinced. An apparent off-shoot from this line in the lower Edinburg is *C.* (*Ceratocephalina*) *tridens* n.subgen., n.sp. In Oranda to lower Martinsburg time there is slight morphological change in the *Diacanthaspis orandensis-cooperi* line.

The ontogeny of certain fossil animals has been interpreted as showing recapitulation of ancestral adult morphology, but no examples of this process have been adduced from trilobites. Following Stubblefield's suggestion (1936), Størmer (1942),

and most vigorously Hupé (1954), have urged that paedogenesis or neotony is an important process in the evolution of trilobites. In the case of *Diacanthaspis* we know the development in detail of the oldest and youngest species (Text-figs. 9, 11; Whittington, 1941, text-figs. 2-6), and something of that of other species (Text-fig. 12). However, not more than one complete ontogenetic series is known from any one of the three lines of descent in *Diacanthaspis*. Thus we do not have sufficient evidence to reveal whether or not recapitulation or paedogenesis are important processes in the evolution, but there are no indications of either being operative. What is clear is that the earliest developmental stages of the various species are remarkably similar, though even at this stage specific differences may be observed. As development proceeds through the meraspid stages the peculiar specific characters of each (long, paired, occipital spines, stout, median, occipital spine, shape of eye lobe, glabellar lobation, etc.) become increasingly evident. Thus the development of species of *Diacanthaspis* affords an excellent example of von Baer's laws (De Beer, 1951, p. 3). Comparison of the ontogeny of *Diacanthaspis* with that of *Apianurus* (Text-fig. 22) and of *Ceratocephala* (Text-fig. 16; Whittington and Evitt, 1954, text-fig. 16) shows that the early meraspid stages are remarkably alike, though generic and subfamily differences are quite evident. As development proceeds the divergence between genera increases. The protaspides of the Middle Ordovician odontopleurids suggest that, if paedogenesis were an important evolutionary process, we might expect, for example, holaspid Devonian odontopleurids to bear fixigenal spines, or to have only basal lateral glabellar lobes, or extremely short, paired, occipital spines. These expectations are not fulfilled. A clearer understanding of the evolutionary processes may be possible when ontogenetic series of later Ordovician, Silurian, or Devonian odontopleurids are known, but present evidence seems not to favour recapitulation or paedogenesis, and seems to suggest that the importance of this latter process in the evolution of trilobites in general may have been overestimated by Hupé (1954) and others.

PART II: SYSTEMATIC DESCRIPTIONS

Family ODONTOPLEURIDAE BURMEISTER, 1843

Diagnosis: Cephalon convex, so that postero-median region stands high above antero-lateral margin. Glabella with maximum width generally at occipital ring, sub-parallel sided or tapering forward, occipital ring may be elongated (sag.) and prominent, lateral lobes may be present, median and/or paired spines or tubercles characteristic; 2-3 pairs of lateral glabellar lobes. Cheek convex, inner posterior corner merges with antero-lateral corner of occipital ring; eye lobe prominent, situated centrally on cheek or inside and behind this point, eye ridge present, anterior branch suture runs forward and inward, posterior branch outward and backward to cross posterior margin, sutural ridges characteristic. Librigenal spine usually stout, broad base merging with postero-lateral borders; commonly row of shorter spines arising from outer edge of border of free cheek, progressively shorter anteriorly; antennular notch in border of free cheek adjacent to anterior branch of suture. Rostrum short (sag. and exs.) and wide (tr.). Hypostome of width greater than, or equal to, length, postero-lateral margins rounded, convex middle body, faint middle furrows running backward and slightly inward from depression at antero-lateral corner of middle body, lateral and posterior border of moderate and similar width, small anterior wing, no wing process, posterior wing extremely small.

Thorax of 8-10 segments, convex axial ring and long articulating half-ring; pleura horizontal, gently or moderately convex, undivided or divided into two bands, long pleural spine on posterior band, directed outward and progressively more strongly backward posteriorly, short pleural spine or spines on anterior band, directed outward and downward. Either or both pleural spines may be missing from the first (and sometimes second) segment because of the size of the facet. Pygidium short, subtriangular in outline, 2 axial rings, may be faint third ring; row of horizontal border spines, one pair often larger than remainder, may be upwardly directed, and with base connected by low pleural ridge across pleural region to first axial ring; or major spine may arise from pleural region.

External surface of exoskeleton rarely smooth, generally with

thorn-like spines or tubercles, granules between them, arrangement of larger spines or tubercles may be symmetrical about midline. Scattered openings occur near tips of large spines (librigenal, posterior pleural, major pygidial), and sometimes also at tips of thorn-like spines or tubercles. Latter may, however, be closed at tip, or may exhibit several tiny openings. Four tiny depressions, arranged at corners of square, may occur at summit of median occipital tubercle.

Doublure narrow, curled under. Appendifers not developed.

Geological Range: Late Lower Ordovician (late Canadian or Arenig) to early Upper Devonian.

Discussion of Systematics of Odontopleuridae

Since Prantl and Přibyl published (1949) their new arrangement of the Odontopleuridae, it has been followed, with some emendation, by Erben (1952a, 1952b), and adopted with reservations by Hupé (1953). Whittington and Evitt (1954, pp. 52-53) voiced some criticisms, and these and others are explained in detail here. Study of the silicified material, and of type specimens of most genera (Whittington, 1956b), has provided a wealth of new data, and my taxonomic scheme is summarized in Text-fig. 3. This adds a new group, but retains the three main groups of Prantl and Přibyl, assigning to them subfamily rather than family rank. I consider the homogeneity of the odontopleurids, as well as the relatively small size of the group, suggestive rather of family than superfamily rank (cf. Hupé, 1953, p. 230). The similarity of early larval stages of different genera may be interpreted as indicating a monophyletic origin for the family and not "at least diphyletic" as maintained by Prantl and Přibyl (1949, p. 131). In subdividing odontopleurids those authors laid emphasis on the form of the cephalon, and particularly the hypostome, the "different origin of the genal spines," and the direction of the posterior pleural thoracic spines. With some of these I agree, while others seem unimportant. I have based the subfamilies here used principally on the following:—

a) Form of the hypostomes, which, while all are of a type peculiar to the family, seem to fall into four sub-types corresponding with the subfamilies (Text-fig. 2).

b) Form and inflation of the glabellar lobes and occipital ring. The characters of this region are of prime importance in sub-

family divisions, and their nature is summarized in the diagnoses.

c) Form of the cheek and position of eye lobe, which together help to determine the course of the dorsal facial suture and the angle between the two branches.

Such features as type of occipital spine or spines, form of thoracic segments, direction of posterior pleural spines, shape of pygidium and development of major border spines seem to me to be of less importance. Whittington and Evitt (1954, p. 32) suggested that the librigenal spine of *Ceratocephala* did not arise in a fundamentally different way from that of *Diacanthaspis,* and further evidence for this view is given here. Thus I do not accept the suggestion that a major systematic division may be based on the supposedly different origin of this spine in different genera (Prantl and Přibyl, 1949, p. 131).

A forward direction of the posterior pleural spines of the first two or three thoracic segments is observed in some miraspinid and in apianurinid genera. In these forms the librigenal spines are well outside the distal parts of the anterior thoracic segments, and so this direction of the pleural spines is possible. In odontopleurinid genera the librigenal spine is sometimes broad-based, and is directed back just outside the distal parts of the anterior thoracic segments. Hence these segments are facetted, and may lack pleural spines, or they are short. This difference in direction of the pleural spines of the anterior thoracic segments was regarded as important taxonomically by Prantl and Přibyl, but it is really dependent on the form of the cephalon, and in my view of little taxonomic value (cf. Whittington and Evitt, 1954, p. 52).

Subfamily ODONTOPLEURINAE BURMEISTER, 1843
(=Odontopleuridae of Prantl and Přibyl, 1949)

Diagnosis: Greatest width of glabella at occipital ring, tapering forward slightly or moderately: occipital ring may be elongated, median or paired tubercles or spines. Eye lobe far back, variable distance out across cheek, angle between two branches of suture near eye lobe 90-120°. Librigenal spine slim to stout, row of border spines on cheek well-developed. Hypostome (when known) slightly wider than long, middle furrow commences in front of mid-length and runs inward at a low angle; shoulder sharp. Lateral notch shallow. Pleurae of thorax

with broad (exs.), convex, posterior band, continuous with stout posterior pleural spine. Pygidium usually with major pair of border spines, 1-2 pairs small border spines between them.

Geological Range: Middle Ordovician to early Upper Devonian.

Discussion: Prantl and Přibyl (1949, pp. 135, 151, etc.) divided this group into two parts, the first (their Odontopleurinae) including *Odontopleura*, *Acidaspis*, *Primaspis*, *Radiaspis* and *Diacanthaspis*. In this group the anterior branch of the facial suture is said to run just outside the eye ridge, so that no subtriangular area is enclosed between suture, eye ridge and the anterior cephalic margin. In the second group (their Acanthalominae) which included *Leonaspis* and *Dudleyaspis*, a striking subtriangular area was claimed to be developed. Text-figures 4, 5, 7, 10, 13, 14 suggest that such an area is variously developed in all these genera, and that it scarcely affords a basis for a subfamily division. An additional distinction between the two groups was the "configuration of the occipital ring and the origin of the occipital spines" (Prantl and Přibyl, 1949, p. 135). I do not regard such differences as of this high a value. An example of our different points of view is our treatment of *Dudleyaspis*. Prantl and Přibyl (1949, pp. 171-172) regarded this genus as allied to *Leonaspis* because of the presence of the subtriangular area enclosed between the anterior branch of the suture and the eye ridge. This area seems to me to be no larger than that in *Acidaspis*, and the glabella lobation and cephalic form of these two genera are extremely similar, and I therefore regard them as allied, and *Dudleyaspis* as derived from *Acidaspis*.

Genus ODONTOPLEURA Emmrich, 1839

Text-figure 4.

Type Species: *Odontopleura ovata* Emmrich, 1839 (=*O. prévosti* Barrande, 1846). See Prantl and Přibyl, 1949, p. 135.

Discussion: Only the type and one very similar species, from the Wenlockian of Europe, are known. *Odontopleura* is distinguished from *Leonaspis* (Text-fig. 7) by the larger, more elevated, lateral glabellar lobes (particularly the basal pair), the elevation and elongation of the median part of the occipital ring, which bears paired spines, the faintly defined occipital lobes,

the smaller eye lobes, situated farther outward and forward, and consequent different direction of the anterior branch of the suture, the slim librigenal spine and more numerous lateral border spines, the long anterior pleural spine and slimmer, less backwardly directed posterior pleural spine of the thorax, and the relatively wider (tr.) pygidium.

In glabellar lobation, convexity of cheeks, position of eye lobes, course of facial sutures, etc. *Odontopleura* approaches

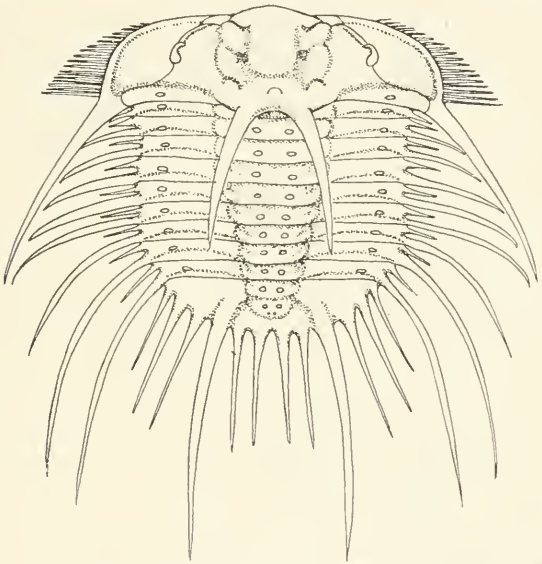


Figure 4. *Odontopleura ovata* Emmrich, Middle Silurian, Motol Beds, e_{a2}, Bohemia. Reconstruction, dorsal view, X 1⅓. Based on MCZ 4170, Butovice; MCZ 4164, Lodenice.

Primaspis (Text-fig. 5), but is distinguished by the form of the occipital ring and stouter occipital spines.

Prantl and Přibyl (1949) reproduced some of Barrande's drawings and also new photographs, but all these illustrations are of specimens flattened in shale, as is that of Hupé (1953, fig. 134). In my drawing I have endeavoured to portray the convex cephalon in its true relation to the thorax, using uncompressed specimens from Butovice, Bohemia.

Genus PRIMASPIS R. and E. Richter, 1917

Text-figure 5.

Type Species: *Odontopleura primordialis* Barrande, 1846. See Prantl and Přibyl, 1949, p. 144.

Diagnosis: Glabella with small third lateral lobes, greatest width across occipital ring and basal lobes, occipital ring not greatly inflated or lengthened, bearing median tubercle or paired spines, small occipital lobes. Eye lobe far back and at about half width of cheek. Lateral border spines short, librigenal spine broad at base. Thorax of ten segments, posterior pleural band inflated at fulcrum and continued into stout posterior pleural spine; anterior pleural spine small.

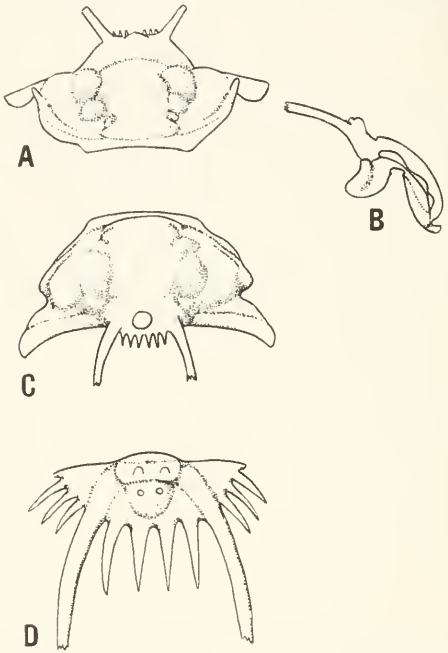


Figure 5. *Primaspis primordialis* (Barrande), Middle Ordovician, Drabov quartzites, dδ, Bohemia. A, B, C, cranidium, anterior, right lateral, and dorsal views respectively, X 3. D, pygidium, dorsal view, X 3. Based on MCZ 4139, Drabov.

Discussion: This genus is represented in Bohemia by species ranging in age from Upper Llandeilo to Ashgill, and perhaps Silurian. *Primaspis keyserlingi* (Barrande, 1846) shows the characteristic features of the genus including the anterior pleural spines, which are not lacking (as stated by Prantl and Přibyl, 1949, p. 14), but is unusual in that the lateral glabellar lobes are fused, there are no occipital spines, and the external surface is smooth. In North America, *Primaspis* is represented by *P. ascitus* n.sp. (described below), *P. trentonensis* (Hall, 1847) (Whittington, 1941, p. 502, Pl. 74, figs. 31-37; Prantl and Přibyl, 1949, p. 149), and probably by *P. crosotus* (Locke, 1843) from the Eden of the Cincinnati district. All these species have a median occipital tubercle, but not paired spines. In the size and convexity of the basal and median lateral glabellar lobes, position of the eye lobe, course of the facial sutures, form of the pygidium, etc., such species as *P. crosotus* approach typical *Leonaspis*, and Prantl and Přibyl (1949, p. 146) have remarked on the *Primaspis* features displayed by *Leonaspis coronata* and *L. deflexa*. This seems to me to point to the derivation of *Leonaspis* from *Primaspis*, as suggested in Text-figure 3. The close relation of *Odontopleura* to these genera has been discussed.

Text-figure 3 also suggests that *Acidaspis* (Text-fig. 13; Whittington, 1956b) is related to *Primaspis*. Such a species as *P. trentonensis*, for example, has a strikingly similar thorax and pygidium, with the posterior pleural bands inflated at the fulcrum, and while the cephalon does not display the special features of *Acidaspis*, it resembles it in having the median lateral glabellar lobe considerably smaller than the basal, in convexity of cheeks, position of eye lobe, course of facial sutures, etc.

PRIMASPIS ASCITUS Whittington, n.sp.

Plates 1 and 2; Text-figure 6

Holotype: USNM 116515 (Plate 1, figures 1, 2, 5, 6); locality 10.

Other Material: Paratypes USNM 116516a-h; all figured specimens in USNM.

Geological Horizon and Locality: Lower Martinsburg shale, locality 10.

Description: Cephalon crescentic in outline, moderately convex

longitudinally, strongly convex transversely. Glabella widest across basal lobes, slightly narrower at occipital ring, narrowing rapidly anteriorly, where it overhangs the border slightly. Occipital ring longest (sag.) medially, where it slopes gently forward to shallow occipital furrow; laterally, behind basal glabellar lobe, a low occipital lobe is developed, defined most clearly on the inner side by a shallow depression. Low median occipital tubercle. Occipital furrow deeper laterally. Three pairs of lateral glabellar lobes, basal (first) largest, sub-oval in outline, inflated and standing above part of median lobe separating them; second lobes inflated, defined by basal and second furrows directed inward and backward at about 45°, the basal furrow deepest at the inner end; inner ends of second and basal furrows joined to each other and to occipital furrow by shallow longitudinal furrow; anterior (third) lateral lobes with faint independent convexity, defined by a short, shallow furrow running inward from the antero-lateral corner of glabella. Axial furrows faint beside glabella, where fixed cheek merges with antero-lateral corner of occipital ring, clearly defined beside lateral lobes, dying out anteriorly where eye ridge merges with glabella. Narrow anterior border separated from glabella by shallow furrow. Cheek most strongly convex in inner corner inside eye lobe, which is situated at about half width (tr.) and close to posterior margin, opposite posterior portion of basal glabellar lobe. Palpebral lobe short, low, defined on inner side by deep palpebral furrow which curves around behind eye lobe and dies out. Anteriorly palpebral lobe and furrow merge with broad eye ridge and furrow on inner side. Eye surface with facets faintly discernible on inner side (Pl. 2, fig. 22). Anterior branch of suture runs forward and then curves inward a short distance outside eye ridge, crosses border furrow on low sutural ridge and meets rostral suture at edge of border. Posterior branch runs in "S" curve back from eye lobe, out across cheek, crosses border furrow on sutural ridge, and runs over border to doublure beneath base of librigenal spine. Anterolateral border of cheek moderately convex, margin curves forward just outside anterior branch of suture. Row of short border spines, increasing in length posteriorly, directed down and slightly out from lower surface of border. Posterior border narrow (exs.) beside occip-

ital ring, widening and swelling outward to merge with the broad base of the librigenal spine. Doublure of cephalon of same width as border. Low projections formed by inwardly projecting outer part of occipital furrow and the three glabellar furrows, particularly the deeper, inner part of the basal furrow. Small depression, with sharply raised anterior edge, in doublure in front of librigenal spine (Pl. 1, fig. 4), is the socket for fulcral process of anterior segment of thorax. Rostrum unknown, but evidently a transverse plate on outer edge of anterior border, perhaps curled under at hypostomal edge. Hypostome slightly wider than long, gently convex middle body, middle furrow running backward and inward a short distance from circular depression at antero-lateral corner, macula faintly defined by convexity, tips of crescentic posterior lobe slightly inflated. Narrow anterior border not defined by furrow; lateral border with small, triangular anterior wing directed dorsally, small lateral notch and sharp, swollen shoulder projecting outward; postero-lateral border widest, gently convex, small median projection in faint, wide median notch. Doublure extending between shoulders, of same width as borders, posterior wing a small, twisted projection (Pl. 1, fig. 18), inner edge of doublure curled in in medial portion. External surface of exoskeleton tuberculate, except in deeper parts of furrows, anterior border (which is granulate), inner part of posterior border, median area of posterior lobe of middle body of hypostome and adjacent maculae, and doublure (except median part of hypostomal doublure). Tubercles vary in size, larger ones may display symmetrical arrangement, including 5 or 6 pairs on fronto-median lobe, some on lateral lobes, and fixed cheek inside eye lobe. Toward tip of genal spine (Pl. 2, fig. 10) tubercles become longer and distally directed, and there appear to be tiny openings at the base on the distal side of some of them. Other tubercles closed at top. Median occipital tubercle with 4 tiny depressions (not the openings of canals through the exoskeleton) arranged in a square, and sometimes a small central pit (Pl. 2, figs. 21, 23).

Number of thoracic segments unknown. Convex axial ring narrowest in mid-line, where it slopes gently forward to deep articulating furrow. Latter with steep anterior slope, articulating half-ring long (sag.). Horizontal pleurae divided by slightly

diagonal pleural furrow into gently convex anterior band and strongly convex posterior band. Anterior pleural spine blade-like, shorter on anterior segments, facet at antero-lateral corner of segment. Posterior pleural band becomes more swollen distally at fulcrum, and is extended into spine, which is short on anterior segments, progressively longer and more backwardly directed on succeeding segments. Ring process and socket well developed, but axial socket and process inconspicuous. Anterior surface of pleura is flattened, with a projecting rim along the upper edge, and this surface fits against the flattened surface of the posterior flange, the projecting rim fitting against and above the curved upper edge of the posterior flange (Pl. 1, figs. 12, 13). Doublure extends in to fulcrum, and has an anterior projection, the fulcral process, which fits into the notch (with raised anterior edge to act as a "stop") in posterior part of doublure (Pl. 1, fig. 15). Axis of pygidium with strongly convex first ring, articulating furrow and half-ring as in thorax, second axial ring lower and less convex, tip of axis merging into border. Pleural regions flat, bounded by a low border anteriorly, strongest antero-laterally, and a broader, more convex postero-lateral border; crossed by a strong ridge connecting first axial ring to the base of major border spine. Five smaller spines, longest posteriorly, project horizontally from postero-lateral border and one major spine (with a swollen base which merges with proximal part of fourth horizontal spine) arises from upper, outer part of posterior border and projects upward and backward. Doublure curled under, as wide as border, at tip of axis most strongly curled and with a slight inward projection, inner, anterior corner forming fulcral articulating process. External surface of thorax and pygidium tuberculate, tubercles densely packed on axial rings, posterior pleural spines and pygidial border spines, less closely packed in articulating furrow and on pleurae and pleural regions, and absent from upper surface of posterior pleural band, articulating half ring, and inner part of doublure. On under side of proximal parts of spines tubercles smaller. Conspicuously larger tubercles as pair on posterior slope of axial ring, including two rings of pygidium, and a third pair (or row of 3) close together at the tip, suggesting a third segment. Large tubercles also in row along anterior pleural band, and one at

about half width (tr.) of posterior band, on posterior slope. Towards tips of thoracic posterior pleural and pygidial border spines tubercles elongated and distally directed, and some openings occur at bases of these tubercles. Elsewhere tubercles closed, and particularly the larger ones appear to expand slightly distally to give a bulbous tip.

Discussion: Primaspis ascitus n.sp. is extremely similar to *P. trentonensis* (Hall; see Whittington, 1941, pp. 501-502, Pl. 74, figs. 31-37) from the Trenton, Sherman Fall formation, of New York and Ontario. It differs from *P. trentonensis* in various minor ways, of which the more obvious are: 1) the greater convexity of the posterior part of the cephalon, so that the posterior surface of the basal glabellar lobes and fixed cheeks, particularly, is longer and descends vertically; 2) the inflation at the fulcrum of the posterior pleural band of the thorax is less; 3) the major border spines of the pygidium of *P. trentonensis* are farther apart, and the base does not merge with the distal part of the minor border spine inside it, but is separate. Also in *P. trentonensis* there are two minor border spines in front of the major spine, not three. Tubercles on the external surface are similarly developed and distributed in the two species, and the median occipital tubercle of *P. trentonensis* exhibits the four tiny depressions. Paired tubercles can scarcely be distinguished on the axis of *P. trentonensis*, except on the posterior edge of the two pygidial axial rings.

Development: Smallest cranidium of length (sag.) 0.6 mm. Text-figure 6A (cf. Pl. 2, figs. 1, 2) summarizes the characters: glabella narrow (tr.), almost parallel sided, basal lobes outlined, faint second lateral glabellar furrows, median occipital tubercle, large median tubercle (with a suggestion of a subdivision indicating that it will later divide and form axial spines 2a) opposite basal glabellar lobes, 3 distinct pairs of tubercles in front (axial spines 2-4); palpebral lobes about opposite axial spines 3, strong eye ridge running forward to antero-lateral corner of glabella, posterior border well-defined, widening (exs.) outward; tubercles on fixed cheeks and border in sub-symmetrical arrangement, including A_1, B, and C. Next largest cephalon known (Text-fig. 6B; Pl. 2, figs. 5, 6), length (sag.) 0.85 mm., shows considerable change. Both the cephalon as a whole, and individual parts,

are more convex. Fronto-median glabellar lobe now steep-sided, standing highest, basal and median lateral lobes well defined and inflated, width of glabella across basal lobes now 35 per cent width of cranidium, rather than 22 per cent as at the smaller stage. Eye lobe opposite anterior part of basal glabellar lobe, fixed

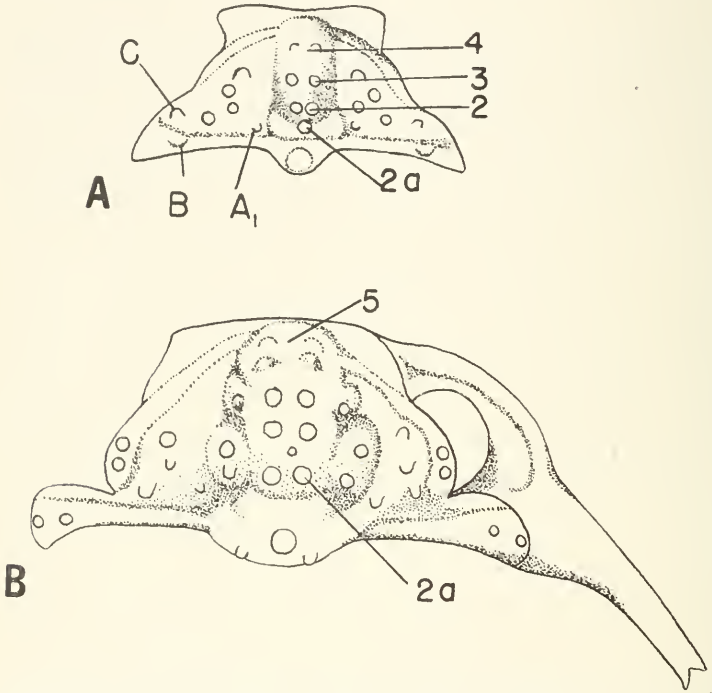


Figure 6. *Primaspis ascitus* n.sp. A, small cranidium, exterior view, drawn from original of Plate 2, figure 2. B, cranidium and right free cheek, exterior view, drawn from original of Plate 2, figure 6, and free cheek of appropriate size. X 38. Spines numbered and lettered as in Text-figure 1.

cheek inflated at inner corner, which merges with occipital ring. Median occipital tubercle large, low; on posterior margin of occipital ring prominent pair of tubercles, other pairs of smaller tubercles in front of these. Five pairs of tubercles on median glabellar lobe — axial 2a, 2-5 — the most anterior not quite sym-

metrical, paired tubercles on lateral lobes, larger tubercles on fixed cheeks and border sub-symmetrically situated. A larger cranidium of length (sag.) 1.2 mm. (Pl. 2, figs. 11, 12) shows that these trends of change have continued — convexity of lateral glabellar lobes and inner part of fixed cheek have increased, and fixed cheek and basal glabellar lobes are level with median glabellar lobe in transverse line. Width across basal lobes now 44 per cent width of cranidium. Eye lobe farther back, paired tubercles, including four on median glabellar lobe, may still be distinguished. In this size of cranidium, third lateral glabellar lobes and occipital lobes are distinct, as are 4 pits in median occipital tubercle. Further increase in size shows slight change continuing, so that width across basal glabellar lobes may become almost 50 per cent of that of cranidium; basal glabellar lobes are inflated sufficiently to stand above part of median lobe between them (Pl. 1, fig. 5); posterior slope of fixed cheek becomes steeper. The conspicuous larger tubercles of earlier stages lose their prominence and cannot be readily picked out in larger specimens. The smallest hypostome (Pl. 2, figs. 3, 4) differs little from larger ones.

Only transitory pygidium known (Pl. 2, fig. 9) is probably stage holaspid-1, since the portion behind the first segment is like the true pygidium, lacking only the first two lateral border spines. The axis is convex, each ring with a pair of prominent tubercles on the posterior edge — recalling the pair on the posterior margin of the occipital ring. Small true pygidia are like larger ones, but may have four border spines in front of the major spines, the anterior extremely short. In larger specimens this small anterior border spine is reduced, presumably with enlargement of the facet, and disappears.

Genus LEONASPIS R. and E. Richter, 1917

Text-figure 7.

R. and E. Richter (1952) regard as undesirable the revival of Conrad's (1840) name *Acanthaloma* by Prantl and Přibyl (1949, p. 151). I am in agreement with them, and have submitted a proposal for the suppression of this name to the International Commission on Zoological Nomenclature.

Type Species: *Odontopleura leonhardi* Barrande, 1846.

Diagnosis: Glabella as wide across large basal glabellar lobes as across occipital ring, two pairs glabellar lobes, the anterior

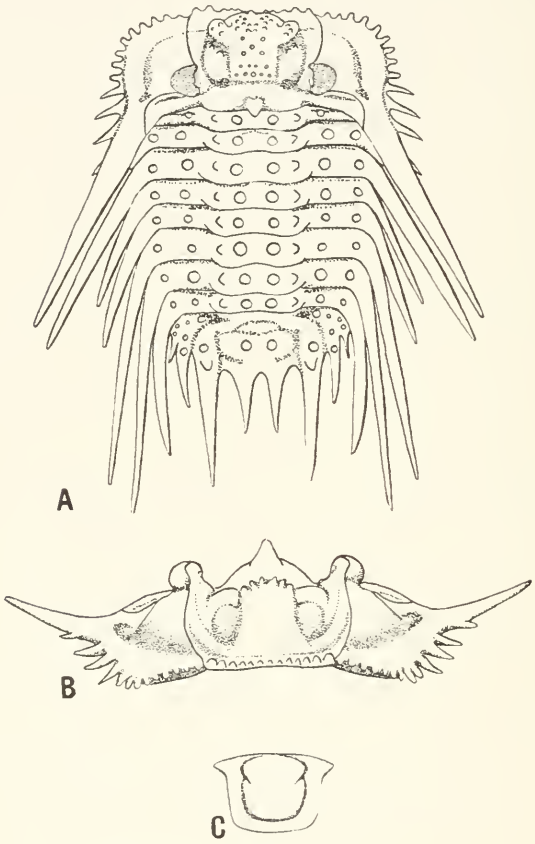


Figure 7. *Leonaspis* new species, Lower Devonian, Haragan shale, Arbuckle Mts., Oklahoma. A, complete exoskeleton, dorsal view. B, cephalon, anterior view. C, hypostome, exterior view. X 2. Drawn from originals of Whittington 1956b, Plate 57, figures 10-16.

smaller than the basal, occipital ring not greatly lengthened or inflated, median tubercle or short median spine. Eye lobe opposite posterior part of basal glabellar lobe or occipital furrow, large to medium size; two branches of suture almost at right angles adjacent to eye lobe, cross border furrows on sutural ridges. Librigenal spines broad-based. Thorax of 8-10 segments, pleurae with anterior pleural spines short, may be bifid distally, posterior band continuous with stout posterior pleural spine; anterior two or three segments may be facetted and pleural spines reduced. Pygidium usually with prominent pair major border spines, one or two pairs small border spines between them.

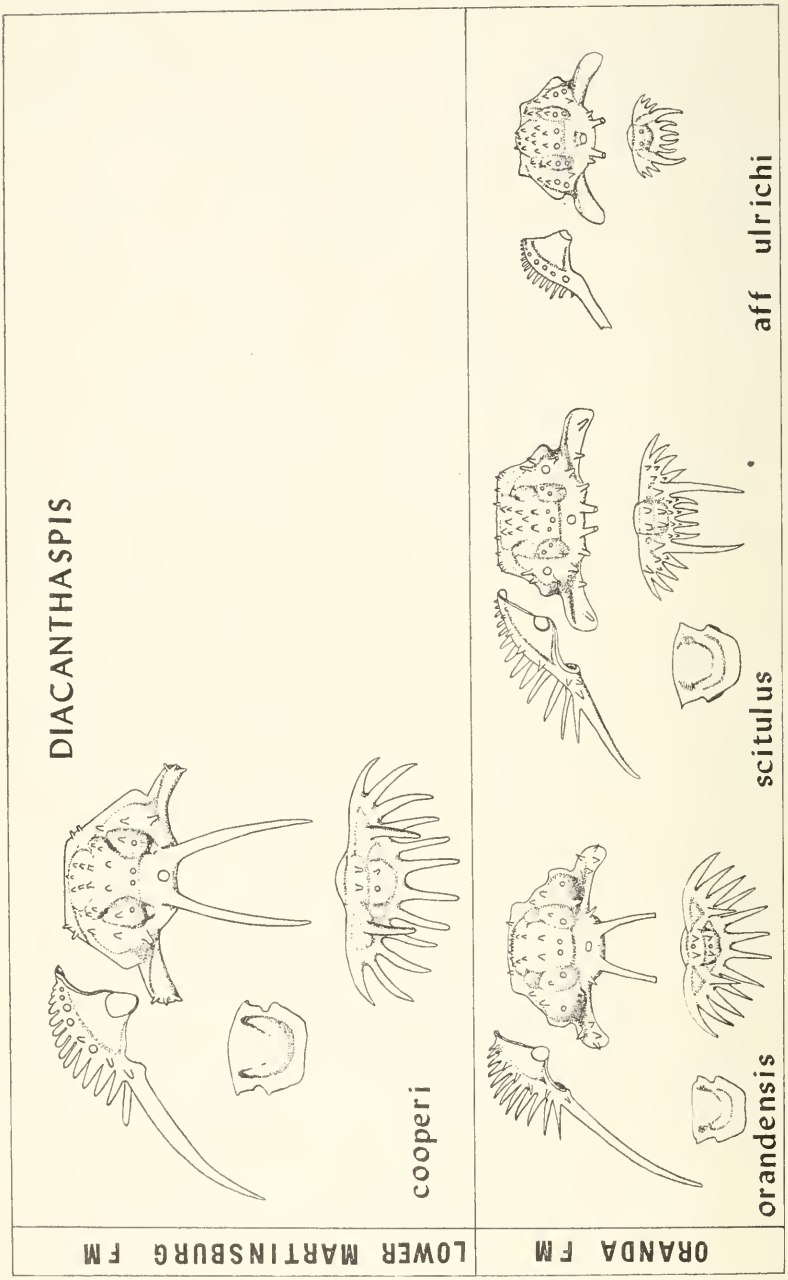
Geological Range: Lower Silurian to Middle Devonian.

Discussion: Elsewhere (Whittington, 1956b) I have described two American species of *Leonaspis*, and one is illustrated here (Text-fig. 7). Both are very like the type species. I have also discussed the genus, and the unsatisfactory nature of the basis for the two subgenera of *Leonaspis* recently proposed by Prantl and Přibyl.

Genus DIACANTHASPIS Whittington, 1941

Type Species: *Diacanthaspis cooperi* Whittington, 1941.

Diagnosis: Glabella widest (tr.) across occipital ring and basal lobes, length (sag.) greater than maximum width; two pairs of lateral lobes, of which the anterior pair is the smaller, sometimes faint, tiny third lateral lobes; occipital ring with paired and median spines, of which one median and/or one pair may be conspicuously longer and thicker than the remainder; small lateral occipital lobes may be present. Eye lobe situated well inwards opposite basal glabellar lobe, sutural and eye ridges distinct. Row of spines on anterolateral cephalic border. Librigenal spine may be hooked at tip. Hypostome shield-shaped, width (tr.) across anterior wings and shoulders about equal; may be circular hole through doublure of shoulder. Number of thoracic segments unknown; pleurae with narrow anterior and broad posterior bands, latter not inflated at fulcrum. Pygidium


DIACANTHASPIS
LOWER MARTINSBURG FM
ORANDA FM
cooperi
orandensis
scitulus
aff ulrichi

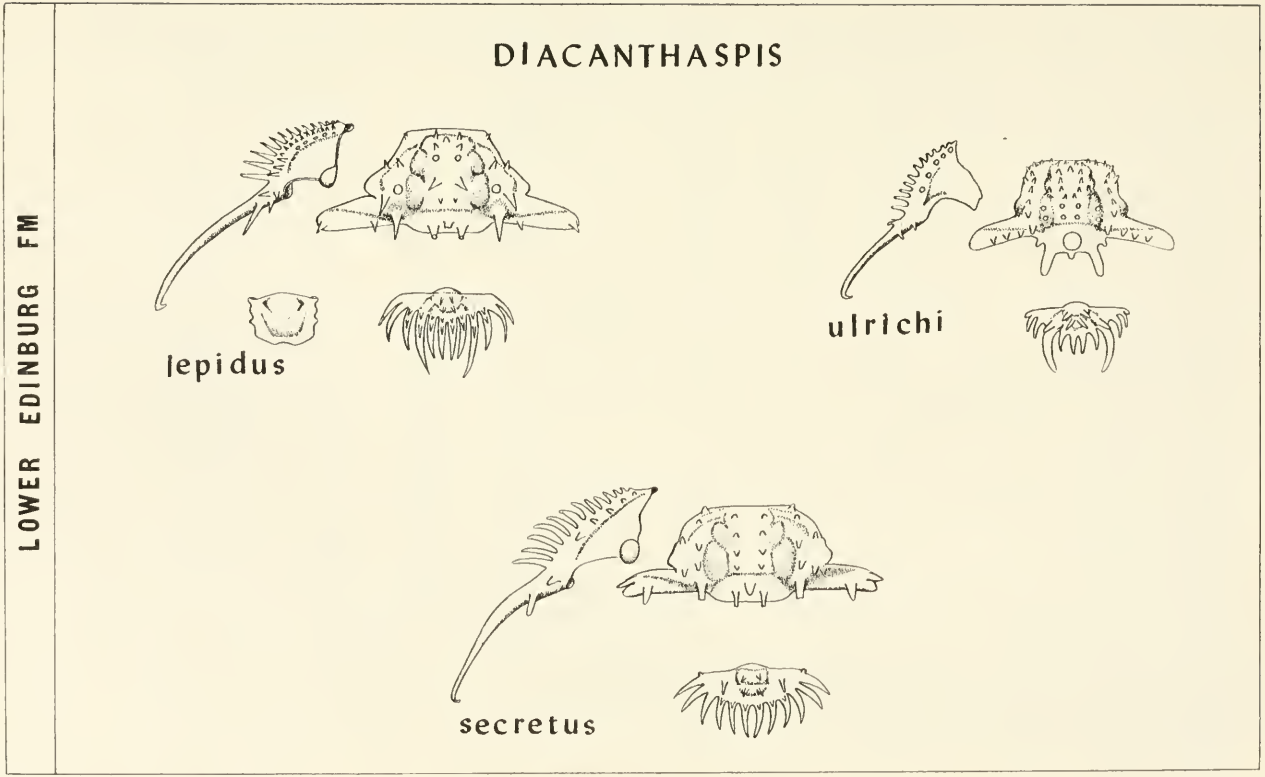


Figure 8. Comparison of species of *Diacanthaspis* in Middle Ordovician formations of Shenandoah Valley, Virginia. *D. lepidus*, *D. secretus*, and *D. ulrichi* are contemporaneous in the lower part of the Edinburg formation. Exterior views, main spines only shown on external surface. Approximately X 10.

of three segments, two axial rings distinct. Border with 6 or 7 pairs of horizontally directed spines, of which the 4th may be elongated; upwardly and backwardly directed major spine may be present on upper surface of border postero-laterally; major spines linked by ridge to first axial ring.

External surface of exoskeleton with median and symmetrically situated thorn-like spines on axial and pleural regions. granulation between these spines.

Geological Range: Middle Ordovician.

Discussion: The diagnosis has been emended to embrace the type and the new species shown in Text-figure 8. A recently described Scottish species (Tripp, 1954, pp. 663-664, Pl. 1, figs. 24-29) also lacks large paired occipital spines and major spines on the pygidial border, but appears to belong here. It also has faint third glabellar lobes, and such faint lobes are seen in *D. scitulus* n.sp. On the other hand, three Esthonian and Swedish species placed in this genus by Prantl and Přibyl (1949, p. 150) are here placed in *Apianurus* n.gen., and I consider it unlikely that "*Acidaspis*" *tremenda* Barrande, 1852, belongs in *Diacanthaspis*, as suggested by Prantl and Přibyl (1949, p. 150).

The similarities between *Diacanthaspis* and *Primaspis* have previously been commented on (Whittington, 1941, p. 502; Prantl and Přibyl, 1949, p. 150), and the similarities and contrasts are well illustrated by the Virginia species described here. The third glabellar lobes are clearly developed in *Primaspis*, and species of this genus have stout major pygidial spines. The inflation of the posterior pleural band at the fulcrum and of the outer part of the posterior cephalic border and base of the librigenal spine, are also characteristic of *Primaspis*, but not of *Diacanthaspis*.

The silicified species, though distinct from each other, have much in common, and they also fall into groups related in time — *lepidus* — *secretus* — *scitulus*, *orandensis* — *cooperi*, and *ulrichi* — aff. *ulrichi*, as discussed in Part I. These groups give a glimpse of the evolving plexus of *Diacanthaspis*, and might be regarded as subgenera, though this step is not taken here. The basic unity of all the species is shown by the similarity between the develop-

mental stages of each, a similarity which is most marked in the earliest stages. The basic unity is also shown by the presence of many common characters which are differently developed in different species, e.g. a relatively large median occipital spine is present in the tiny cranidia of *D. secretus* and *D. ulrichi*, but in the former it loses its prominence in later stages, while in *D. ulrichi* it is retained to the adult. The development of the paired occipital spines, present in all the young stages, offers another such example.

In all the species of *Diacanthaspis* there is a deep depression separating the basal glabellar lobe from the outer part of the occipital ring, the slope down to the depression from the occipital ring being gentle, that from the glabellar lobe steep. In *D. orandensis* and *D. cooperi* the forward-sloping antero-lateral part of the occipital ring develops a low, subcircular rise, bearing one or two thorn-like spines. This is the occipital lobe, a faintly developed feature peculiar to these two species.

The spines and granules on the external surface of the different species are described and illustrated in detail, and have been discussed in general terms in Part I. It should be emphasized that only in the best preserved specimens is the tip of the thorn-like spines seen to be truncated by a disk in which are tiny pits or openings. Their arrangement is not as regular as that of the four pits at the tip of the median occipital spine, and it seems unlikely that they are different-sized versions of the same structure.

DIACANTHASPIS COOPERI Whittington, 1941

Plate 3; Plate 9, fig. 6; Plate 11, figs. 16-18; Text-figures 8, 9.

Geological Horizon and Localities: Lower Martinsburg formation, localities 9-12.

Description: The new material enables the following additions to be made to the original description (Whittington, 1941, pp. 502-508, Pl. 74, figs. 1-30, text-figs. 2-6).

The eye surface is preserved in some specimens (Pl. 3, fig. 21; Pl. 11, fig. 17), the outer surface with the tiny facets faintly convex, corresponding pits on inner surface deeper. Librigenal spine ends in a sharp point, not a hook (Pl. 3, fig. 20).

Slightly larger hypostomes (Pl. 3, figs. 7, 9, 10, 13, 14) than those described previously have a length (sag.) little more than two-thirds the maximum width across the anterior wings. There is a distinct lateral notch, and the shoulders are sharply pointed, the tip directed ventrally. The doublure is widest near the shoulder, the inner edge extended in a small ventrally-directed posterior wing. There is a circular hole through the doublure at the shoulder. Posteriorly the doublure is narrowest. Ornament of granules, but coarse tubercles on tips of crescent-shaped posterior lobe of middle body, and along posterior margin.

Segments from all parts of thorax now known (Pl. 3, figs. 11, 12, 15, 16) but not complete number. The anterior segment (Pl. 3, fig. 11), since it fits behind the cephalon, lacks the anterior, and has an extremely short posterior, pleural spine. The articulating half ring is, however, larger and more convex than that of posterior segments. The photographs show the progressive increase in size of both pleural spines in successive segments, as well as the changes in direction.

Axis of the pygidium (Pl. 3, fig. 19) with two rings and a pair of spines at the tip, suggestive of a third segment. The base of the large, upwardly directed spine on the margin of the pleural region is situated between the bases of the 3rd and 4th pleural spines, and is connected by a low ridge to the first axial ring.

Photographs at high magnifications (Pl. 9, fig. 6) show the dorsal external surface of the exoskeleton covered with symmetrically situated thorn-like spines with granules between. The granulation is absent only from the posterior edge of the

Figure 9. *Diacanthaspis cooperi* Whittington. A, B, Protaspis, dorsal and ventral views, drawn from the original of Plate 3, figures 1, 2. In A, the right free cheek has been drawn in its correct position rather than displaced as in B and the original. In B, the outline of the poorly preserved hypostome is indicated by a broken line. C, Stage 0 exoskeleton with only right free cheek restored in position. Drawn from original of Plate 3, figure 3, and free cheek of appropriate size. D, small cranidium and left free cheek drawn from originals of Plate 3, figure 8. Approximately X 62. Paired spines numbered and lettered as in Text-figure 1; Lb is librigenal.

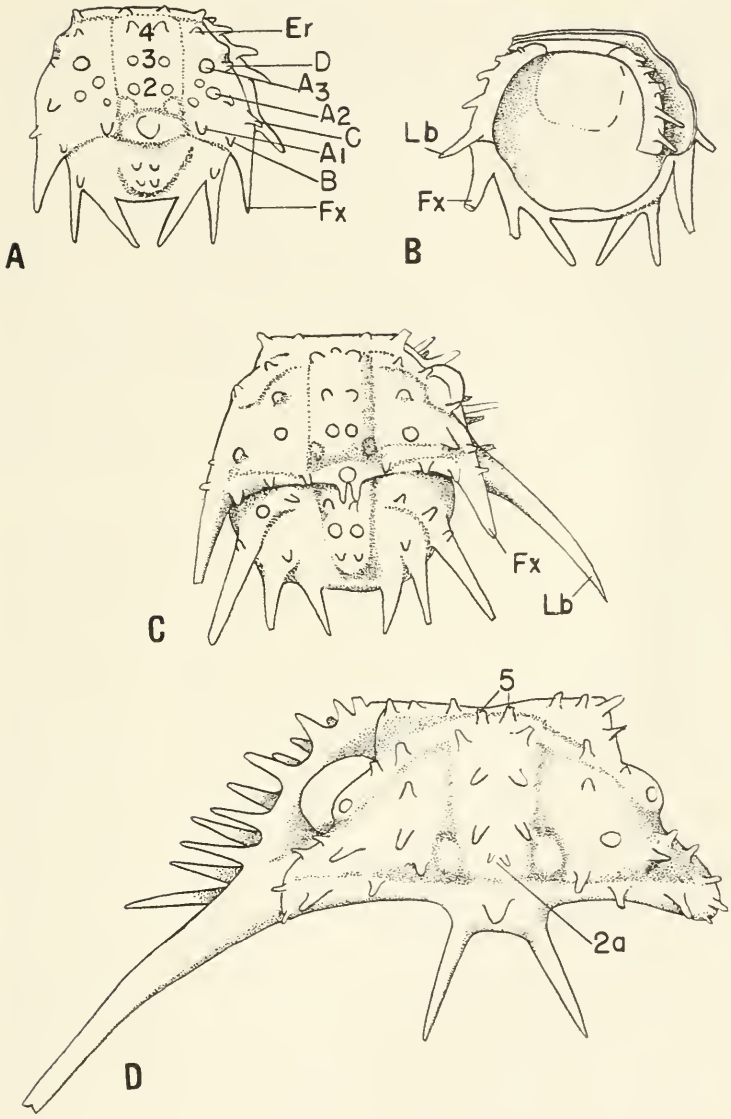


Figure 9

occipital ring, the upper part of the posterior cephalic border, corresponding edge of the thoracic axial rings and the posterior pleural bands, the border of the pygidium and the raised ridge on the pleural regions, and the paired occipital, librigenal, and posterior pleural spines. Distally directed openings may be seen on the occipital and librigenal spines, and between and on the granules at the tips of the lateral cephalic and pygidial border spines openings were present (Pl. 11, fig. 16). The thorn-like spines, when not obviously broken, appear bluntly rounded at the tip, with a distinct, tiny central opening surrounded by an irregular ring of tiny depressions or openings (Pl. 9, fig. 6). The median occipital tubercle is short and bluntly rounded at the tip, and some specimens show four depressions, arranged in a square, on the slopes of the tip (Pl. 11, fig. 18). These appear to be depressions, not openings through the exoskeleton, and resemble those seen in, for example, *D.* aff. *ulrichi* n.sp. and *D. orandensis* n.sp. (see below).

Development: Protaspis (Pl. 3, figs. 1, 2, 5, 6; Text-fig. 9 A, B) of length (sag.) 0.42 mm., maximum width (tr.) at base of fixigenal spines 0.51 mm. Shield subcircular in outline, gently convex, most strongly so anteriorly; divided by faint, curving transverse furrow into larger cephalic and smaller pygidial portion; doublure narrowest posteriorly. Glabella outlined by broad, shallow furrows, gently convex, a median occipital and three pairs (2, 3 and 4 of Text-fig. 9A) of axial spines; occipital furrow faint, in front of outer parts pair of extremely faintly defined, subcircular, basal lateral lobes. Cheeks slope quite steeply antero-laterally, connected by narrow anterior border; low eye lobe far forward and outward, almost in line with axial spines 4. Eye surface not preserved. Free cheek narrow, the two branches of the suture forming a straight line on the dorsal side, curving across the doublure as shown in Text-figure 9B. Posterior border not clearly defined, extended into long, broad-based fixigenal spine. Short spines or tubercles arranged symmetrically on cheeks and anterior border include A_1, A_2, A_3, B, C, D, Er, two pairs on the anterior border, and additional small tubercles on the fixed cheek. Five spines on vertical margin of free cheek, posterior (librigenal) the longest. Protopygidium with strongly convex axis, especially posteriorly, bearing two pairs of tubercles. Pleural regions depressed near

axis, convex toward rolled border; two stout pairs of border spines, outer pair with spine at base, inner pair directed backward and inward. Rostrum and hypostome poorly preserved (Pl. 3, fig. 2), general outline as suggested in Text-figure 9B.

Exoskeleton at Stage 0 (Pl. 3, figs. 3, 4; Text-fig. 9C) of length (sag.) 0.57 mm., width (tr.) at base fixigenal spines 0.6 mm., length (sag.) of cephalon 0.34 mm. A dissociated free cheek of appropriate size has been drawn in position in Text-figure 9C. Glabella parallel-sided, more convex, defined by deep axial furrows; deeper occipital furrow and ring relatively wider, with large median tubercle and slimmer but longer paired spines; low median tubercle in front of axial spines 4. Tiny basal lateral glabellar lobe faint, almost concealed by increased inflation. Cheek more convex, eye lobe larger and farther back, course of cephalic suture similar. Posterior border defined distally, fixigenal spines as long as in protaspis. Tubercles (or short spines) as on protaspis, on posterior border additional spine between A_1 and B. Free cheek with librigenal spine stouter and longer than fixigenal, five spines on edge of border, decreasing in size forward. A new row of spines has appeared on the border, outside and below the other, directed outward and downward, extending to base of librigenal spine and increasing in length posteriorly. Transitory pygidium (width (tr.) at anterior margin 0.5 mm.) with well-defined axis, pleural regions flat with rolled border. Three pairs of spines on axis, and three on borders, inner directed slightly inward. First interpleural furrow faint, two spines on pleura, outer at base of border spine, third small spine on outer side border spine near base. Upright spine at base second border spine.

Smallest cranidium previously described (Whittington, 1941, Pl. 74, fig. 1; text-fig. 2) slightly larger than those of Stage 0, and without trace of fixigenal spines. A cephalon of length (sag.) 0.51 mm. is here restored (Text-fig. 9D; Pl. 3, fig. 8) and is at same stage of development as original of my 1941, Plate 74, fig. 2 and text-figure 3. Basal part of glabella wider, basal glabellar lobes much larger, axial spines 2a have appeared, as have axial spines 5 (in place of the median tubercle of Stage 0). Eye lobe larger and farther back, but most striking is absence of fixigenal spine, so that librigenal spine is at genal angle.

There are no specimens showing any transition (e.g. a reduction of the genal spines) between Stage 0 and this stage.

The smallest transitory pygidium previously described (Whittington, 1941, p. 508; Pl. 74, fig. 11) is probably that of Stage 1, while the larger one (op. cit., p. 508; Pl. 74, fig. 12, 13) may belong to a stage between 1 and 8. A new specimen (Pl. 3, figs. 17, 18) appears to belong to Stage 8 (assuming that the holaspid thorax is composed of 10 segments). Anterior segment defined by interpleural groove, and right posterior pleural spine curves backward and slightly inward. Proximal portions of the posterior pleural spines of second segment may be seen, and inside them there are four pairs of small marginal spines. On the right side (the left is broken off), just inside the margin, is a long upwardly and backwardly directed spine, its base in line with the fourth pair of spines on the axis. The inclination of this spine is different from that of the posterior pleural spines, and it appears to be the upwardly directed major pleural spine so characteristic of the true pygidium. On the posterior pleural bands of the first two segments are two short spines, upwardly directed, the outer at the base of the posterior pleural spine, and forming a curved line between the axial ring and posterior pleural spine. A spine corresponding to this outer spine is present on the pleural portion of the third segment, just in front of the upwardly directed major pleural spine. The curve between the axis and the base of the major spine corresponds with that of the first two segments, and suggests that the major pleural spine is the modified posterior pleural spine of the first segment of the true pygidium.

DIACANTHASPIS LEPIDUS Whittington, n.sp.

Plates 4, 5; Plate 7, figure 15; Text-figures 8, 10

Holotype: USNM 116517 (Pl. 5, figs. 1, 4, 7, 9), locality 2.

Other Material: Paratypes USNM 116518 a-c; all figured specimens in USNM.

Geological Horizon and Localities: lower Edinburg limestone, localities 2, 3, 4.

Description: At the localities given above, two species of *Diacanthaspis* occur, *D. lepidus* n.sp., and *D. secretus* n.sp., the

latter described below. Material from these localities, collected at different times, has been prepared, and the relative frequency of occurrence of parts of the adult exoskeleton is as follows (counts of complete or nearly complete parts only):

TABLE 1

Numbers of Exoskeletal Parts of Two Species of *Diacanthaspis* at Localities 2-4.

	Locality 2	Locality 3		Locality 4
	Cooper Collection	Evitt Collection	Cooper and Whittington Collection	Evitt and Whittington Collection
D. lepidus n.sp.				
Cranidia	41	112	45	14
Free cheeks	48	185	20	8
Pygidia	78	122	12	14
D. secretus n.sp.				
Cranidia	57	24	4	14
Free cheeks	75	30	—	15
Pygidia	98	14	—	12

The rarity of *D. secretus* at locality 3, and the fit of the free cheeks, has led to the associations made here (Text-fig. 8), and support is afforded particularly by the nature of the ornament. No specimens are intermediate in morphology between those here called *D. lepidus* and *D. secretus*, and there is little variation in even minor features of the ornament between individuals of either species. It might be suggested that these two morphological types, occurring together, are sexual dimorphs of one species, rather than two distinct species. The fact that *D. secretus* is rare at locality 3, but occurs in almost equal numbers to those of *D. lepidus* at localities 2 and 4, seems to argue against this suggestion.

Diacanthaspis lepidus is considerably older than the type species, *D. cooperi*, and is distinguished from it at once in lacking the

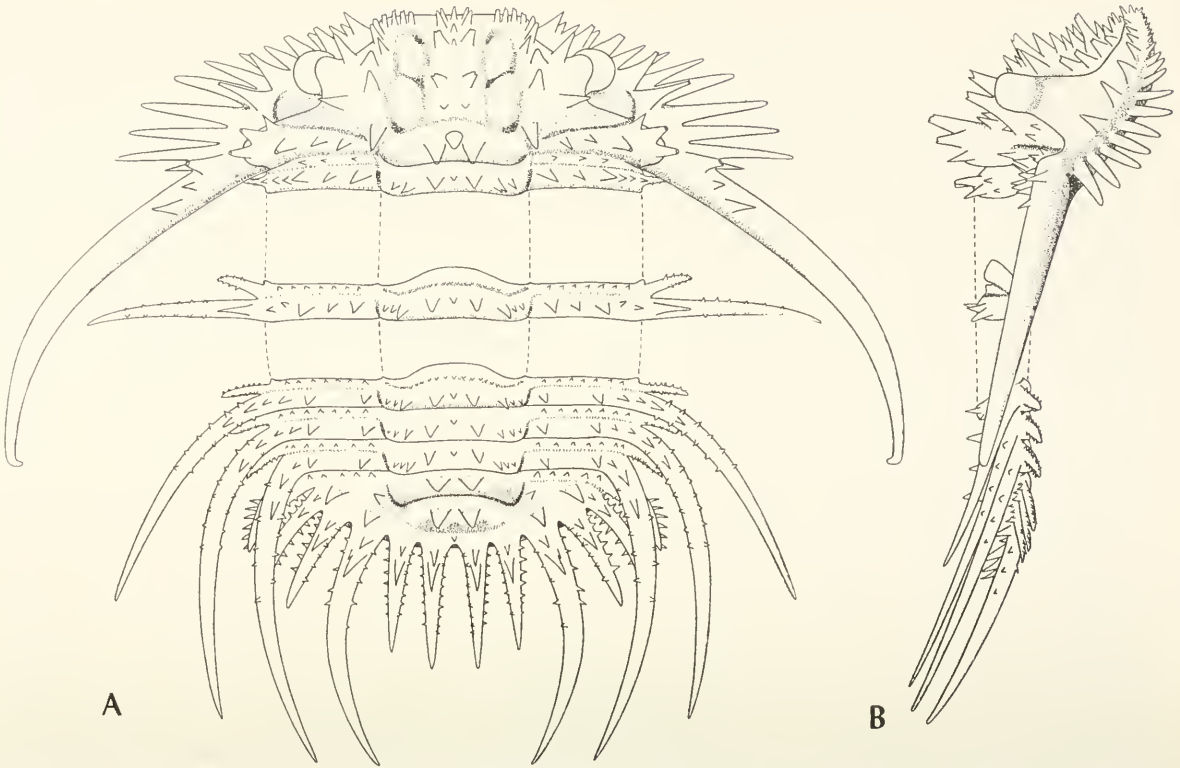


Figure 10. *Diacanthaspis lepidus* n.sp. Reconstruction, A, dorsal, B, right lateral views. Number of thoracic segments unknown. Approximately X 12.

stout occipital spines. The cephalon is less convex transversely, and both the width (tr.) between the palpebral lobes, and of the occipital ring, are lesser fractions of the cranidial width. Occipital lobes are absent. Tip of librigenal spine hooked. The pygidium of *D. lepidus* is relatively shorter than that of *D. cooperi*, and has the elongated fourth marginal spines. That of *D. cooperi* has a long upwardly-directed spine situated on the border inside the base of the fourth marginal spine, which latter is not elongated. One hypostome from locality 3 is referred to *D. lepidus*, since this is the common species at this locality. It is of the same general type as that of *D. cooperi* (compare Pl. 3, figs. 7, 9, 10 with Pl. 5, figs. 15-17), but different in detail — e.g. the outline of the lateral and posterior margins, depth of lateral notch, projection of shoulder directed laterally rather than ventrally, greater convexity of middle body, and shorter middle furrows. The doublure is incomplete postero-laterally, but at the shoulders it shows no circular opening.

The long thorn-like spines on the external surface are hollow, and the tips of even the longest and best preserved are not pointed, but cut off (Pl. 7, fig. 15). The end is usually open, but in some is covered by a plate having several tiny holes or depressions in it (Pl. 4, fig. 22). Openings, directed distally, occur on the librigenal spines, tips of the cephalic outer border spines, on the posterior pleural spines of the thorax, and near the tips of the pygidial border spines. These openings may have been occupied by sensory hairs. On the cephalon, between the thorn-like spines, the external surface is granulate, except on the convex surface of the borders and occipital ring. Similarly, granulation is absent from the convex surface of the axial rings, the posterior pleural bands, and the border of the pygidium.

Development: A series of cranidia down to the length (sag.) 0.48 mm. is shown in Plate 4, figures 8-10, 12-14, 16-18. The smallest (Pl. 4, fig. 6) is distinguished from that of a smaller size of *D. secretus* n.sp. (Pl. 6, fig. 12; Text-fig. 11C) by the presence of a median, as well as small paired, occipital spines, faint basal glabellar lobes, a less marked indentation in the anterior margin, a slightly different arrangement of the spines on the fixed cheek on and inside the palpebral lobe (spines A_2, A_3, D, and Er), and a tiny additional spine at the extremity

of the posterior border near the posterior edge, between spines B and C. In cranidia of 0.5-0.66 mm. in length (compare Pl. 4, fig. 7, with Pl. 6, figs. 14, 15), some of these differences are more pronounced — the smaller indentation in the anterior margin in *D. lepidus,* the different arrangement of the spines referred to on the fixed cheek and the additional spine on the posterior border. The first two of these differences persist into larger sizes, and aid in differentiating the species. Another specific character already evident at this size is the different shape of the palpebral lobe. In larger cranidia the differences between *D. lepidus* and *D. secretus* become more pronounced.

All the tiny cranidia with fixigenal spines (probably Stage 0) known from localities 3 and 4 are of the type shown in Plate 6, figures 6, 7 (cf. Text-fig. 11B), i.e. all the spines are long, with a thick base and bluntly terminated tip, there is a single occipital and axial pairs 2, 3, and 4, and the anterior margin is indented. This type is so like the cranidial portion of the protaspis from locality 4 shown in Plate 6, figures 1-5 that the conclusion that they form part of a series is inevitable, and this series is traced into the holaspid *D. secretus.* However, a second protaspis known from locality 4 (Pl. 4, figs. 1-5) is clearly odontopleurid, and differs from that of *D. secretus* only in the following characters: (a) the spines on the dorsal surface are low, appearing rather as high tubercles; (b) the occipital ring bears a median spine and a suggestion of small, paired spines just behind the median spine; (c) small basal glabellar lobes are present; (d) axial spines 5 are represented by tiny tubercles. The characters (a), (b), and (c) are those which distinguish the smallest known cranidium of *D. lepidus,* the spines on the external surface being less massive than those of *D. secretus.* Axial paired spines 5 are not known in this size of *D. lepidus* cranidium, but there is a median axial 5. This second protaspis from locality 4 is thus tentatively regarded as that of *D. lepidus,* for comparison between it and smallest known cranidia of other species of *Diacanthaspis,* and of *Ceratocephala, Apianurus* n.gen., and *Calipernurus* n.gen., reveals far greater differences.

Diacanthaspis secretus Whittington, n.sp.
Plate 6; Plate 7, figures 1-14; Text-figures 8, 11.

Holotype: USNM 116519 (Pl. 7, figs. 1, 3, 5, 11), locality 2.

Other Material: Paratypes USNM 116520 a-d; all figured specimens in USNM.

Geological Horizon and Localities: lower Edinburg limestone, localities 2, 3, 4.

Description: The occurrence of this species is discussed under *D. lepidus* n.sp. The seemingly minor but persistent differences that distinguish *D. secretus* from *D. lepidus*, summarized in Text-figure 8, are: 1) the longer, lower palpebral lobe, more strongly curved course of the anterior branch of the suture, and better-defined eye-ridge (compare Pl. 5, figs. 1, 4, 7, with Pl. 7, figs. 1, 3, 5); 2) the different direction and arrangement of the four long spines on the fixed cheek between the palpebral and lateral glabellar lobes (compare Pl. 5, fig. 1 with Pl. 7, fig. 1); 3) the backward curve of the tips of the outer spines on the border of the free cheek, and the lesser number of spines on the upper surface of this border (compare Pl. 5, fig. 9 with Pl. 7, fig. 7); 4) the relatively longer pygidium, in which the fourth marginal spines are not elongated (compare Pl. 5, fig. 12 with Pl. 7, fig. 10). A single small ornamental spine, upwardly directed, is present at the base of the 4th, 5th, and 6th marginal spines; in *D. lepidus* two such spines are present on the 3rd, 4th, 5th, and 6th marginal spines. Other ways in which the exoskeletal parts of the two species can be discriminated may be seen from a study of Plates 5 and 7. It will be seen that the minor ornamental spines of *D. lepidus* tend to be longer and sharper, as well as more numerous in certain regions (compare Pl. 5, figs. 1, 7, 9 with Pl. 7, figs. 1, 3). The thorax of neither species is completely known, but isolated segments of *D. secretus* have shorter, blunter ornamental spines, and the lateral barbs on the anterior pleural spine are fewer (compare Pl. 5, figs. 2, 3, 10, 11 with Pl. 7, figs. 4, 6).

The librigenal, cephalic, thoracic pleural and pygidial border spines of the exoskeleton show openings (Pl. 7, figs. 12-14) like those described in *D. lepidus*. The thorn-like spines have the tips cut off and closed, with tiny openings or pits in the end. The granulation is distributed as in *D. lepidus*. Intermediate between the thorn-like spines and granules are high tubercles, and these apparently are closed at the tip.

Development: Metaprotaspis (Pl. 6, figs. 1-5; Text-fig. 11A)

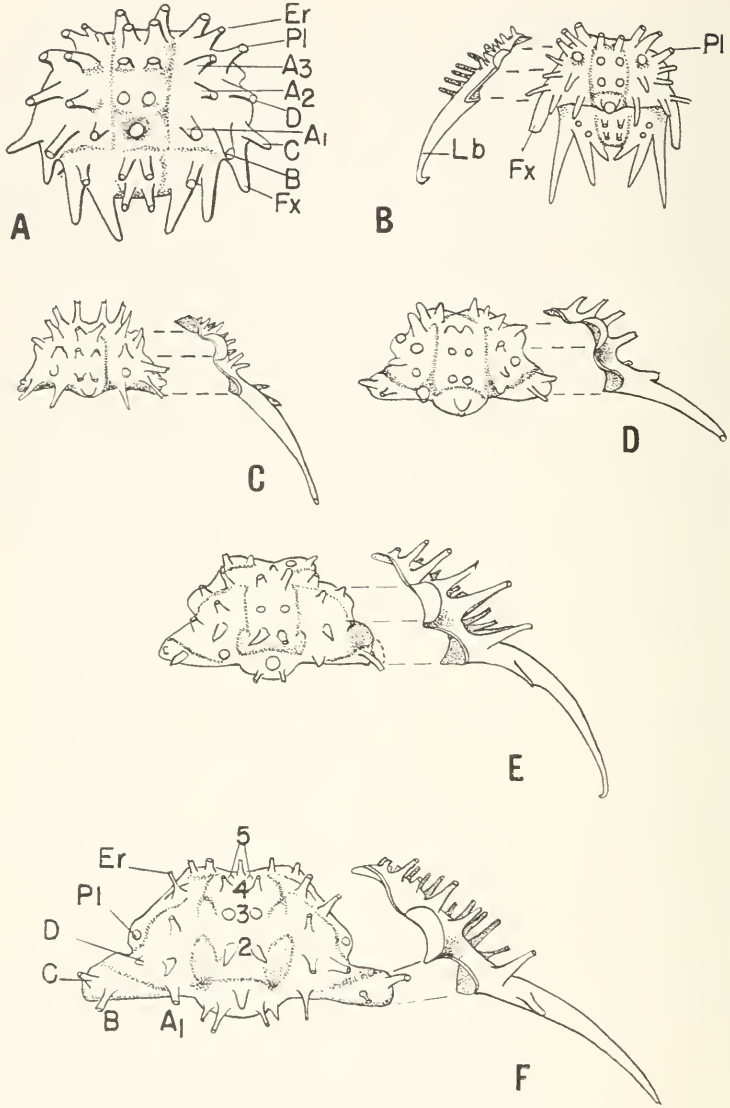


Figure 11

subcircular in outline, gently convex; free cheeks, rostrum and hypostome unknown. Cranidial portion divided by shallow, broad, poorly-defined axial furrows into glabella, with very gentle convexity, and gently convex fixed cheeks. Glabella not divided into rings, but with stout median occipital spine and three pairs in front, a fourth pair on the anterior border, these four pairs forming two lines diverging slightly forward. Posterior area of cheek with prominent spines on dorsal surface symmetrically arranged, lettered A_1, A_2, A_3, B, C, D, in Text-figure 11A. At margin, at end of curving row formed by median occipital and spines A_1 and B, is posteriorly directed fixigenal spine. On anterior area of cheek, spines included are those labelled Pl, A_3, and Er respectively in Text-figure 11A, and one on anterior border. Anterior margin faintly indented at midline. Only a gentle slope divides cranidium from protopygidium. Axis prominent, two pairs of spines, two horizontal pairs directed back from margin of pleural regions, and one pair on dorsal surface at base anterior marginal spine.

Stage 0 specimen reconstructed (Text-fig. 11B) from originals of Plate 6, figures 6, 10, and similar specimens. It is larger in size (length (sag.) about 0.5 mm., length cranidium 0.32 mm.) but otherwise exceedingly similar, except for the presence of a third pair of border spines on the pygidium. Free cheek extremely narrow (tr.), small eye lobe far forward, row of five spines on upper surface of convex border, row of seven on outer surface of border, long librigenal spine with hooked tip. Rostrum and hypostome unknown. Text-figures 11C-F (cf. Pl. 6, figs. 8, 12, 14, 15) show larger cranidia and associated free cheeks. Not until the cephalon is about 0.5 mm. in length (sag.) (Text-fig. 11E, Pl. 6, fig. 14) do small paired occipital spines appear, faint

Figure 11. *Diacanthaspis secretus* n.sp. A, Protaspis, dorsal view, drawn from the original of Plate 6, figures 1-4. Approximately X 52. B, Stage 0, dorsal view, left free cheek separated from cranidium, drawn from originals of Plate 6, figures 6, 10. Approximately X 32. C, D, E, F, cranidium and right free cheek of individuals of increasingly larger size, exterior views. Drawn from originals of Plate 6, figures 8, 9, 12, 14, 15 respectively. Approximately X 32. Paired spines numbered and lettered as in Text-figure 1; Lb is librigenal.

basal glabellar lobes, and a median axial spine in front of axial spines 3. The eye has moved back at this stage, and considerably farther back at the next stage shown, when the second lateral glabellar lobes and axial spines 5 appear (Text-fig. 11F; Pl. 6, fig. 15). The indentation in the anterior margin is marked in small cranidia but becomes much less obvious, though not quite obliterated, as size increases. Additional paired spines appear on cranidia of length (sag.) about 1 mm. (Pl. 6, fig. 16) upwards. A slightly larger transitory pygidium than Stage 0 (Pl. 6, fig. 13) has three pairs of spines on the axis, the border with three pairs of spines directed horizontally (posterior pleural spines), progressively shorter backward. At the antero-lateral corner is the broken base of a tiny anterior pleural spine. On the pleural region a short spine is situated at the base of the first two posterior pleural spines, remainder of region granulated, and showing the first pleural furrow and interpleural groove. A considerably larger transitory pygidium (Pl. 6, fig. 20) shows 4 pairs of axial spines and 4 posterior pleural spines. Short, blade-like anterior pleural spines are present on the first three segments (mostly concealed in dorsal view); there are two spines on the posterior pleural band of the first segment, the outer one longest.

Discussion of Ontogeny of *Diacanthaspis*

If these ontogenetic series of *D. lepidus* and *D. secretus* be accepted, it is remarkable that the protaspis of the latter (Pl. 6, figs. 1-5) has far the more massive and prominent spines on the external surface, while the reverse is the case in the holaspis, where the spines, though massive, are fewer and shorter and thus less prominent than the long, thin, thorn-like spines of *D. lepidus* (compare Pl. 7, figs. 3, 15). Comparison of the metaprotaspis and Stage 0 specimens of *D. lepidus* and *D. secretus* with corresponding specimens of *D. cooperi* (Pl. 3, figs. 1-6; Text-figs. 9A-C) reveals the close similarity — in outline and form, shape of glabella, presence of fixigenal spines, number and arrangement of spines on the external surface, and axial and border spines of the protopygidium. Distinctive of *D. secretus* is the size of the spines on the external surface, while in both the others these spines are short and rounded. In *D. lepidus* and

D. cooperi basal glabellar lobes are present in the metaprotaspis. Comparison between later developmental stages (Pl. 4, figs. 6-10, 12-14, 16-18; Text-figs. 9D, 11C-F; Whittington, 1941, text-figs. 2-6) reveals both the parallelisms and specific divergence. Fixigenal spines are lost abruptly in all. In *D. secretus* lateral glabellar lobes and axial spines 2a and 5 appear at a later stage than in either of the other species. While paired spines are present on the occipital ring of the older species, they never become bigger than the median occipital tubercle, whereas in *D. cooperi* their growth is rapid.

Diacanthaspis ulrichi Whittington, n.sp.

Plate 8; Text-figures 8, 12.

Holotype: USNM 116521 (Pl. 8, figs. 1-5), locality 7.

Other Material: Paratypes USNM 116522a-c; all figured specimens in USNM.

Geological Horizon and Localities: lower Edinburg limestone, localities 3, 4, 7. This species has not been found at locality 2, and only 2 pygidia are known from locality 3. From locality 4, 8 cranidia and 14 pygidia, together with 26 immature cranidia, have been recovered. At locality 7 *D. ulrichi* is not accompanied by *D. lepidus* and *D. secretus*, whereas at locality 4 these latter two species are rather more abundant (see Table 1, p. 217) than is *D. ulrichi*.

Description: D. ulrichi is readily distinguished from contemporary and later species (except *D.* aff. *ulrichi*) by: (1) the convex fronto-median glabellar lobe and narrow (tr.), low lateral lobes, which latter are separated from the fixed cheeks by extremely faint axial furrows; (2) the straight course of each branch of the suture adjacent to the eye lobe, which gives a distinctive outline to both cranidium and free cheek; (3) the short, thick, bluntly terminated median and paired main occipital spines; (4) the convex axis and outwardly-sloping pleural regions of the pygidium; (5) the short spines on the outer edge of the cheek border and border of the pygidium.

The external surface of the cephalon (Pl. 8, figs. 24, 30) bears, besides the main occipital and outer border spines referred to, smaller, thick, blunt-tipped spines. Inside the cephalic

borders the surface between the spines is covered with fine granules. The blunt spines are symmetrically arranged on the lateral glabellar lobes and cheeks, but on the fronto-median lobe, while the number and general disposition is similar in different specimens, it is not exactly the same, nor is the arrangement symmetrical (Pl. 8, figs. 1, 30). On the posterior edge of the occipital ring (Pl. 8, fig. 24) there is a median and a pair of these spines, and in some specimens a second pair is situated in front of the main pair.

Hypostome unknown.

Pleurae of thoracic segments (Pl. 8, figs. 12, 13, 17, 21) with narrow (exs.) anterior and wide (exs.) posterior band, former bearing short anterior pleural spine, latter bearing larger spine, progressively longer and more backwardly curved on successive segments. Axis with 2 pairs spines, 3 on posterior band, area between smooth; articulating groove, anterior band, and posterior flange tuberculate. Axis of pygidium with two rings, each with pair of spines. Six pairs of spines on outer edge of border, the first very small, the fourth elongated and connected by a low ridge to the first axial ring. Prominent spine on upper surface of border at base of elongated fourth spine. One specimen (Pl. 8, fig. 9) has only one, rather than two, pairs of spines between the major border pair.

The distal portions of the main median and paired occipital spines (Pl. 8, figs. 24, 30) display an irregular, hummocky surface at high magnifications. There may have been openings at the base of the tubercles on the paired spines, and the tip of the median spine shows the four tiny depressions arranged in a square. The distal tips of the posterior outer border spines of the free cheek, and the longer border spines of the pygidium, may have been like those of the paired occipital spines. Other, shorter, spines are rounded at the tip and may be closed, and the distal part of the librigenal spine does not show any openings.

Development: Protaspis unknown. Development of cephalon from Stage 0 shown in Text-figure 12 A-D (compare Pl. 8, figs. 10, 14-16). The smallest cranidium has the characteristic trapezoidal outline, low, parallel-sided glabella divided only by the occipital furrow, low palpebral lobe far forward, faint eye ridge, and fixigenal spine. The presence of the latter suggests

that it belongs to Stage 0. The median occipital spine is represented by a large, low tubercle, and the paired occipital spines, present in some specimens of this size, are tiny. Remainder of glabella without paired spines. On fixed cheeks paired spines A_1, A_2, A_3, B, and C have been recognized. Surface of cranidium between spines covered with fine granules. In the next size of cranidium found, fixigenal spines are absent, the palpebral lobe is farther back, and paired spines 2, 3, 4 appear on the glabella

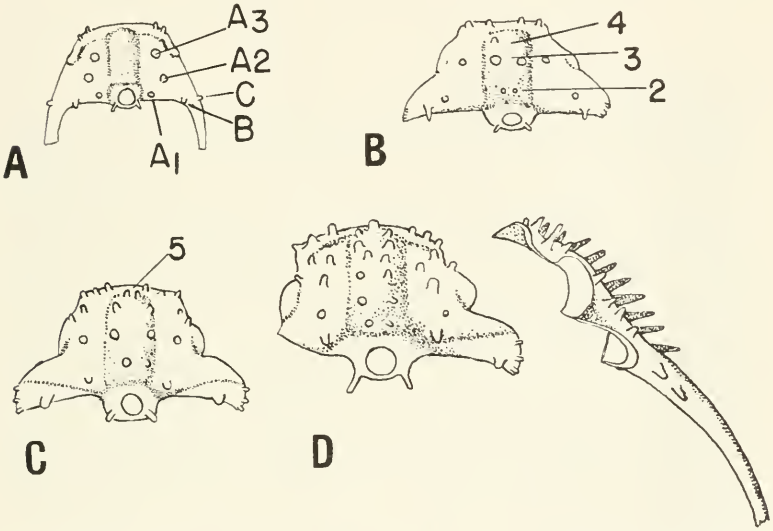


Figure 12. *Diacanthaspis ulrichi* n.sp. A, B, C, D, cranidia of increasing size, exterior views, right free cheek shown in D. Approximately X 38. Drawn from the originals of Plate 8, figures 10, 14, 15, 16, 28 respectively. Paired spines numbered and lettered as in Text-figure 1.

in front of the occipital furrow. At this stage the cranidium is quite like that of *D. cooperi* (Whittington, 1941, text-fig. 2) and *D. secretus* (Pl. 6, fig. 12; Text-fig. 11D), but the large median occipital tubercle and fewer and shorter paired spines on fixed cheeks and borders are distinctive. The later development parallels that of other species, except that beyond a length (sag.) of about 0.6 mm. the symmetrical arrangement of spines on the glabella in front of the occipital ring is lost.

On Plate 8, figures 25, 26 show a transitory pygidium of an unknown stage. Axis with three pairs of spines; two long border spines are posterior pleural spines of two segments that will be released into thorax; anterior pleural spine of first is short, curved. Behind axis, two pairs of tiny border spines. A small holaspid pygidium is shown in Plate 8, figures 22, 23.

Diacanthaspis aff. ulrichi Whittington, n.sp.

Plate 9, figures 1-5, 7-9; Text-figure 8.

Material: all figured specimens in USNM.
Geological Horizon and Localities: Oranda formation, locality 8.

Description: a few fragments only of this extremely rare species are known, and deemed insufficient as the basis for a new specific name. It is like *D. ulrichi* n.sp., but differs (compare Pl. 9, figs. 1, 5, with Pl. 8, figs. 1, 6), for example, in the more convex fronto-median glabellar lobe, the longer median occipital spine, the deeper axial furrows of the cranidium, particularly outside the lateral glabellar lobes, and the more triangular outline of the pygidium. The spines and granules on the external surface of the two species are similar both in appearance and distribution (compare Pl. 9, figs. 7-9 with Pl. 8, figs. 24, 30). The smooth tip of the median occipital spine shows clearly the four depressions arranged in a square. The smooth, blunt tips of the spines on the glabella and free cheeks show a tiny central opening.

Diacanthaspis orandensis Whittington, n.sp.

Plate 10; Pl. 11, figures 1-15, 19, 20; Text-figure 8.

Holotype: USNM 116523 (Pl. 10, figs. 1, 3, 5-7), locality 8.
Other Material: Paratypes USNM 116524a-f; all figured specimens in USNM.
Geological Horizon and Locality: Oranda formation, locality 8. Three species occur at this locality, and approximate numbers of complete or fairly complete parts of exoskeletons obtained are as follows:

TABLE 2

Numbers of Exoskeletal Parts of Three Species of *Diacanthaspis* at Locality 8.

	D. orandensis n.sp.	*D. scitulus* n.sp.	*D.* aff. *ulrichi* n.sp.
Cranidia	120	25	2
Free cheeks	150	38	1
Pygidia	100	31	2

The most common hypostome, 130 specimens, is regarded as belonging to *D. orandensis*, the less common, 16 specimens, to *D. scitulus*.

Description: Diacanthaspis orandensis is exceedingly similar to *D. cooperi*, differing only in minor but persistent characters, of which the more obvious are: (1) relatively longer outer border spines on free cheek and pygidium (compare Pl. 10, figs. 2, 17, 18, with Pl. 3, fig. 19, and Whittington, 1941, Pl. 74, fig. 23); (2) more prominent axis of pygidium; (3) thorn-like spines on external surface tend to be longer and sharper; (4) particularly axial, but also longitudinal, furrows bounding first and second lateral glabellar lobes tend to be deeper and lobes to be more prominent (compare Pl. 10, figs. 1, 3, 5; Pl. 11, fig. 19 with Pl. 9, fig. 6, and Whittington, 1941, Pl. 74, figs. 24, 25, 29). As might be expected, the early developmental stages of the two species are indistinguishable (compare Pl. 11, fig. 1 with Pl. 3, fig. 8); only later do the specific differences become clear.

No complete specimens of the librigenal spines are known, i.e. the extreme tip is always broken, but almost certainly it is not hooked. The dorsal external surface of *D. cooperi* has been described in detail, and most of the remarks apply to *D. orandensis*. Specimens of the latter, however, are better preserved, and there is no doubt of the presence of distally-directed openings, with raised rims, on the paired occipital, librigenal, posterior pleural, and pygidial border spines. On the rounded tip of the median occipital spine of *D. cooperi* tiny depressions, arranged in a square, were observed. Similar depressions are

present on the occipital spine of *D. orandensis* (Pl. 11, fig. 19), and further, the tips of the thorn-like spines are likewise bluntly rounded with a group of tiny depressions, of which the central may be larger (Pl. 11, fig. 19). The depressions are extremely small, and whether or not they are the openings of canals through the exoskeleton is uncertain.

Diacanthaspis scitulus Whittington, n. sp.

Plates 12, 13; Text-figure 8.

Holotype: USNM 116525 (Pl. 12, figs. 1-3), locality 8.

Other Material: Paratypes USNM 116526 a-e; all figured specimens in USNM.

Geological Horizon and Localities: Oranda formation, locality 8.

Description: As Table 2 (p. 229) shows, this species is much less common than *D. orandensis* at locality 8. The general plan of the exoskeleton, and particularly the outline of the glabella, absence of prominent paired occipital spines, and arrangement of thorn-like spines on the external surface of the exoskeleton (and particularly of the fixed cheek), ally it with *D. lepidus* n.sp. and *D. secretus* n.sp. rather than with *D. orandensis* and *D. cooperi*. The lack of large median or paired occipital spines, and the form of pygidium, distinguish it from *D. ulrichi*. *D. scitulus* differs from *D. lepidus* and *D. secretus* in that: (1) the cephalon is more convex transversely between the eye lobes, the eye ridges and sutural ridges are stronger and more clearly defined, and the row of border spines on the free cheek extends back onto the base of the librigenal spine (compare Pl. 12, figs. 1-3 with Pl. 5, figs. 1, 7, 9 and Pl. 7, figs. 1, 3); (2) there are seven pairs of horizontally directed border spines on the pygidium, approximately equal in length, and a stouter, longer spine arises from the upper surface of the border and is directed backward and slightly upward (compare Pl. 12, fig. 14 with Pl. 5, fig. 12 and Pl. 7, fig. 10). In the type of major pygidial spine, convexity of the cranidium, strength of sutural ridges, and extension of lateral border spines on to the base of the librigenal spines, *D. scitulus* approaches the *D. orandensis-cooperi* group (compare Pl. 12, figs. 1-3, 14 with Pl. 10, figs. 1, 3, 5, 27). Thus the species of *Diacanthaspis*, while they fall into groups, never-

theless betray their close relationship. Large specimens of *D. scitulus* show, particularly on the inner surface (Pl. 12, fig. 7), a faintly impressed furrow directed transversely on the anterior glabellar lobe where it slopes down to the second glabellar furrow. This furrow is not well enough developed to be termed a third glabellar furrow, but may be the incipient stage of such a furrow. The hypostome is of *Diacanthaspis* type, and distinguished from that of *D. orandensis* (with which it occurs, but in lesser numbers) by the more curved outline of the anterior margin, the less angulate postero-lateral outline, and the narrower (sag.) posterior border (compare Pl. 13, fig. 8 with Pl. 10, fig. 22). The doublure of the shoulder shows the large circular opening. The one known specimen of the hypostome of *D. lepidus* is of similar type, but does not show the opening through the doublure.

The dorsal external surface of the exoskeleton is shown in Plate 13, figures 12, 14-17. The symmetrically arranged thorn-like spines are truncated and closed at the tip, and there are tiny depressions (which may be openings) in the tip. Granulation extends between the thorn-like spines, but is absent from the cephalic borders, central part of occipital ring and inner corner of fixed cheek around large spine, upper surface of lateral glabellar lobes and eye ridge, axial rings, posterior pleural bands, borders of pygidium and pleural ridge, and border and librigenal spines. Tiny tubercles are present particularly near the tips of the librigenal and border spines. Distally directed openings with a raised rim also occur on the distal parts of these spines, including the tip of the librigenal spine (Pl. 13, fig. 14), which is not hooked as in *D. lepidus*, *D. secretus* and *D. ulrichi*.

Development: The smallest known cranidium of *D. scitulus* is 0.93 mm. in length (sag.) (Pl. 13, figs. 3-5), and is very like cranidia of about the same size of *D. lepidus* (Pl. 4, figs. 12-14) and *D. secretus* (Pl. 6, figs. 16-18), even in the size and position of the main thorn-like spines. On the fronto-median glabellar lobe axial spine pairs 2, 3, 4 are present, a median spine only in the position of pairs 2a and 5. On the fixed cheeks spines A_1, A_2, A_3, B, C, and Pl may be seen. The shape of the palpebral lobe, and the strength of the eye ridge and sutural ridges, are especially distinctive of *D. scitulus*, while examples of smaller dif-

ferences are the greater number of spines on the cranidium of *D. lepidus*, and the fewer and differently situated spines of *D. secretus*. The small free cheeks of *D. scitulus* (Pl. 13, fig. 13) have the distinctive border spines, as also do the small pygidia (Pl. 12, fig. 16).

Genus ACIDASPIS Murchison, 1839

Text-figure 13.

Synonym (objective): *Pseudomonaspis* R. and E. Richter, 1917.
Type Species: by monotypy, *Acidaspis brightii* Murchison, 1839 (Whittington, 1956b).

Diagnosis: Two pairs of lateral glabellar lobes well developed, separated from median lobe by deep longitudinal furrows, in type species frontal glabellar lobe rounded, projecting well in front of anterior lateral glabellar lobes. In Ordovician species small third lateral glabellar lobes are present. Median part of occipital ring inflated and prolonged backward as thick median spine, separated from rest of glabella by shallow median part of occipital furrow; lateral part of occipital ring with low, gently convex occipital lobe in inner corner, behind deeper outer part of occipital furrow. Eye lobe elevated, situated opposite most posterior part of basal glabellar lobe; anterior branch of the facial suture runs straight forward and inward, diverging from the course of the eye ridge, crosses border furrow on sutural ridge and curves over the anterior border. Posterior branch curves downward and outward across the fixed cheek in front of the posterior border furrow, and on to the inner side of sutural ridge, against which this furrow ends. It then curves over posterior border, inside base of librigenal spine. Convex anterolateral border with row of stout spines directed downward, longest posteriorly and diminishing forward; antennal notch present, anterior border between sutures projects slightly. Librigenal spines long, curved. Thorax of 10 segments, posterior pleural band convex and inflated at fulcrum. Pygidium with 7 pairs border spines, 5th the major. External surface tuberculate.

Geological Range: Middle Ordovician to Middle Devonian.

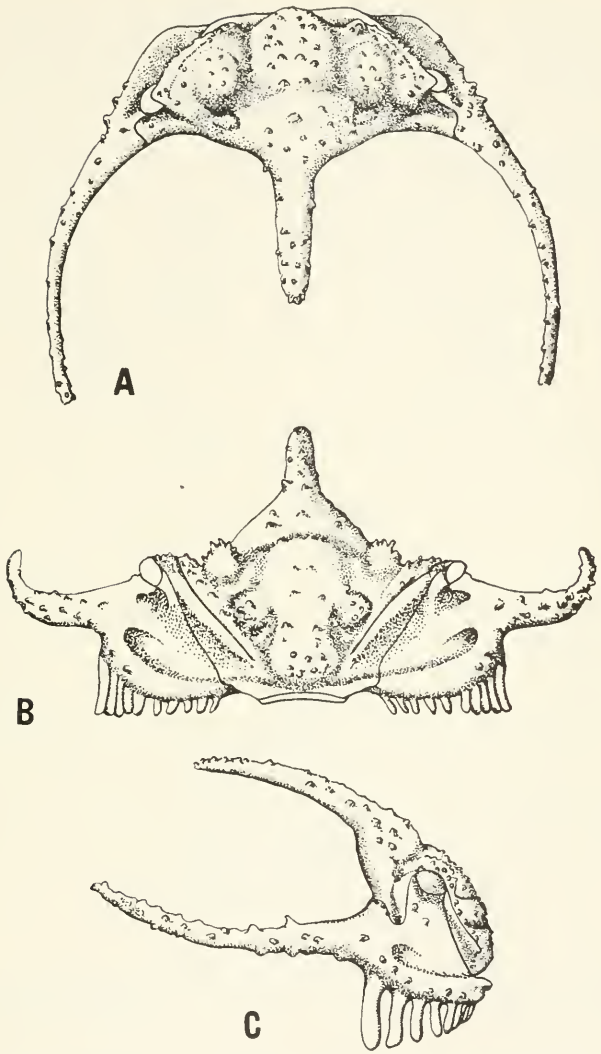


Figure 13. *Acidaspis brightii* Murchison, Wenlock limestone, Middle Silurian, England. A, B, C, cephalon, dorsal, anterior, and right lateral views respectively, approximately X 3. (After Whittington 1956b, text-figure 1.)

Genus DUDLEYASPIS Prantl and Přibyl, 1949
Text-figure 14.

Type Species: *Acidaspis quinquespinosa* Lake, 1896 (Whittington, 1956b).

Diagnosis: Occipital ring with short median spine and two further pairs spines on posterior margin; not prolonged backward and lacking lateral lobes. In front of large basal lateral lobes glabella narrows rapidly; small third lobes, third lateral furrows short, transversely directed, frontal glabellar lobe projecting in front of third lobes. Eye lobe situated opposite mid-

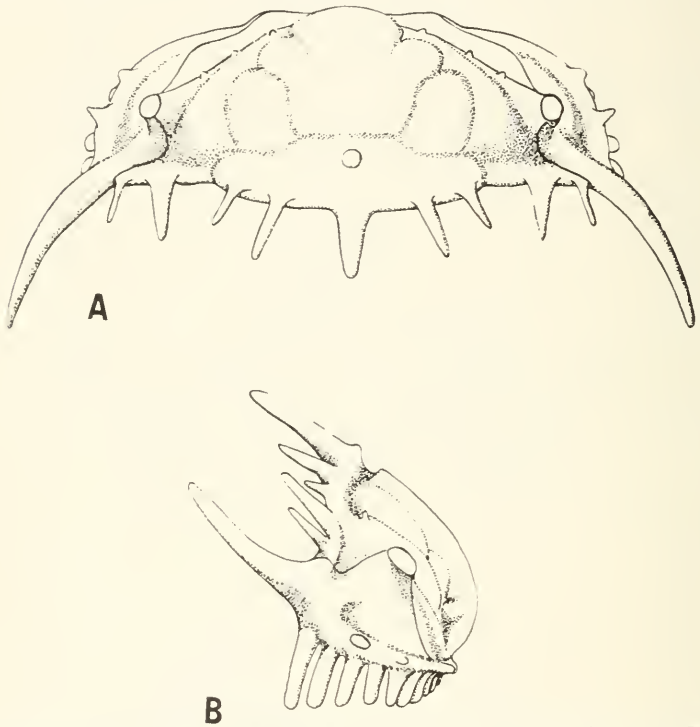


Figure 14. *Dudleyaspis quinquespinosa* (Lake), Wenlock limestone, Middle Silurian, England. A, B, cephalon, dorsal and right lateral views respectively, approximately X 6. After Whittington 1956b, text-figure 2.

part of basal lateral glabellar lobes, anterior branch suture runs on sutural ridge straight forward and slightly inward to anterior border; suture then runs more directly inward and over outer edge of border to meet rostral suture about where anterior border projects forward. Sutural ridge also connects eye lobe and swollen base librigenal spine, and posterior branch suture runs along inner side of this ridge and over border inside base librigenal spine. Convex anterolateral cephalic border with row vertical spines as in *Acidaspis;* librigenal spines slim, curved; two pairs spines on posterior border backwardly directed. Thorax of 10 segments, pygidium with 2 pairs spines between major pair.

Geological Range: Silurian (mainly Middle).

Genus RADIASPIS R. and E. Richter, 1917

Type Species: *Arges radiatus* Goldfuss, 1843 (Prantl and Přibyl, 1949, p. 142).

Discussion: The type species has been described by R. and E. Richter (1917, pp. 468-472, text-figs 9, 10; 1926, pp. 109-110; 1930, text-fig. 2). The form of the cephalon is like that of *Acidaspis* — in convexity, lobation of glabella, elongation of occipital ring, presence of lateral border spines, etc., but is distinguished by the paired occipital spines. The thorax is of 9 segments, and the pygidium is notable for the absence of major border spines (there being 8 pairs of equal length) and the bilobed form of the posterior part of the axis. I regard *Radiaspis* as most closely related to *Acidaspis*, not *Odontopleura*, contrary to Prantl and Přibyl's opinion. The genus is known from Lower to earliest Upper Devonian of Germany and Bohemia.

Subfamily MIRASPINAE R. and E. Richter, 1917

(=Ceratocephalidae of Prantl and Přibyl, 1949; of Erben, 1952)

Diagnosis: Glabella wide; occipital ring long (sag. and exs.), convex, with prominent paired spines arising from swollen base; well-defined, sub-parallel sided median lobe, gently to strongly convex, 2 pairs lateral glabellar lobes, small third pair usually present. Convex cheek of characteristic subrectangular outline,

antero-lateral portion projecting, librigenal spine arising from upper surface of border, directed upward and outward, may or may not be spines on cheek border; eye lobe about centrally situated, may be pedunculate; two branches of suture usually inclined to each other at an obtuse angle. Hypostome subrectangular in outline with median posterior notch; middle furrow in form of triangular depression in anterolateral corner of middle body. Thorax of 9-10 segments; pleurae lacking pleural furrow or divided by it into narrow convex anterior and broader convex posterior bands, anterior pleural spine characteristically blade-like, with lateral barbs, and downwardly directed; posterior pleural spine much larger, horizontal, first 2 or 3 directed outward and in some cases slightly forward, successive spines directed more strongly backward. Pygidium with border spines, may or may not be major pair, may or may not be unpaired median posterior border spine.

Geological Range: Middle Ordovician to Middle Devonian.

Discussion: Since this group includes *Miraspis,* the oldest available name Miraspinae is used for it. Prantl and Přibyl and Erben include here the three best-known genera — *Miraspis, Ceratocephala* and *Dicranurus.* As a result of the present study I include *Proceratocephala, Whittingtonia,* and *Ceratocephala* (*Ceratocephalina*) n.sub.gen. I have no new information on *Ceratonurus, Koněprusia, Orphanaspis,* or *Selenopeltoides,* but presume that they may also belong here. It appears to me to be an overestimate of the value of morphological differences to divide this group into three subfamilies, and some of the criteria used by Prantl and Přibyl — e.g. supposed fusion of facial sutures in *Ceratocephala,* lack of anterior pleural spines of thorax in *Dicranurus* — are either of doubtful value or erroneous.

Genus MIRASPIS R. and E. Richter, 1917

Text-figure 15.

Type Species: *Odontopleura mira* Barrande, 1846. (Whittington, 1956b.)

Diagnosis: Occipital ring with wide (sag.) posterior band. Small third lateral glabellar lobes. Eye lobe situated opposite

mid-part of basal glabellar lobe, pedunculate. Row long, slim spines, diminishing in length forwards, on antero-lateral cephalic border. Nine thoracic segments, well-marked pleural furrow;

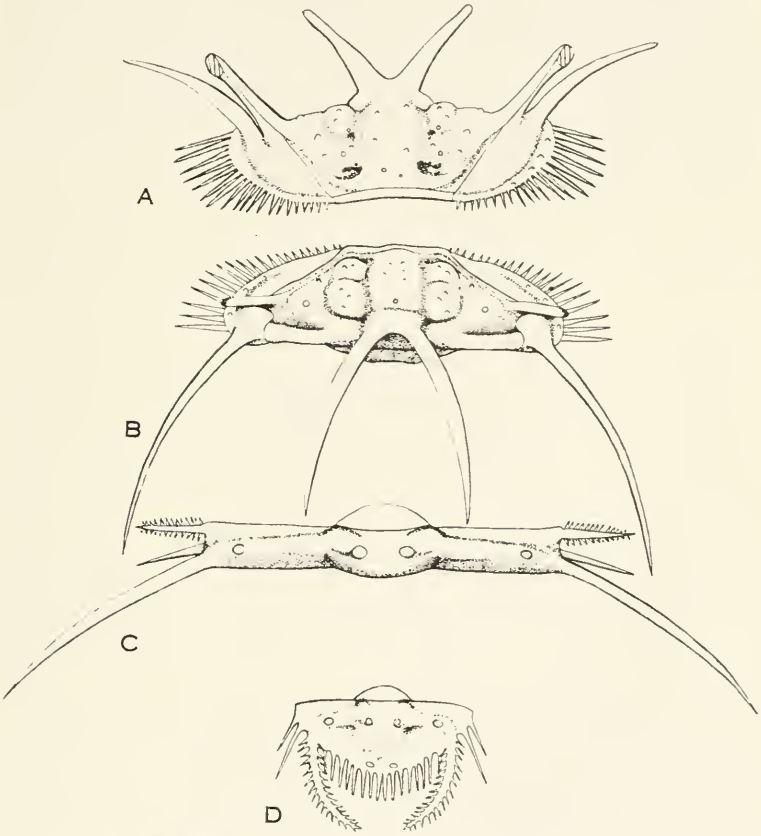


Figure 15. *Miraspis mira* (Barrande), Motol Beds, $e\alpha_2$, upper middle Silurian, Bohemia. A, B, cephalon, anterior and dorsal views, respectively; C, thoracic segment, dorsal view; D, pygidium, dorsal view. Approximately X 1½. After Whittington 1956b, text-figure 3.

slim additional pleural spine between anterior and posterior. Pygidium with pleural ridge running out at first transversely from first axial ring, then turning abruptly to join base of curved

major spine. Four to eight pairs small border spines between major pair, 2 in front.

Geological Range: Middle (?) Ordovician to Lower Devonian.

Discussion: In addition to the material described elsewhere is the single silicified pygidium discussed below, and the incomplete thorax and *Miraspis*-type pygidium from the Middle Ordovician of Wales (Whittington and Williams, 1955, p. 425, Pl. 40, fig. 119). Complete exoskeletons of Ordovician odontopleurids with *Miraspis*-type pygidium are as yet undescribed, so the range of the genus is uncertain.

?Miraspis sp.ind.

Plate 14, figures 1, 7.

Material: one incomplete pygidium and one free cheek, both from locality 3, lower Edinburg limestone.

Discussion: The pygidium is of characteristic *Miraspis* form, the short, convex axis with a prominent first ring, bearing a pair of spines. Pleural region crossed by a ridge connected to the axial ring, this ridge directed at first outward and then turning sharply to merge with the base of the major border spine. In front of ridge is first pleural furrow, separating it from low convex band bearing row of three spines. Major border spine long, directed backward and slightly upward, two small spines outside the major spine, 4 pairs inside, upper surface of border with small spines, most prominent pair behind axis. Small spines scattered on pleural regions.

The free cheek has the librigenal spine arising from the upper surface of the border, latter bearing a row of short spines, and the eye lobe is pedunculate. These features recall *Miraspis,* and suggest that possibly this cheek belongs to the same species as the pygidium.

Genus Ceratocephala Warder, 1838

Synonyms (subjective): *Onchaspis* (*Onychaspis*) Raymond, 1925; see Whittington and Evitt, 1954, p. 53. *Trapelocera* Corda, 1847; see Prantl and Přibyl, 1949, pp. 180-181, for summary of argument.

CERATOCEPHALA LACINIATA Whittington and Evitt, 1954

Plate 14, figures 2-6, 8-15; Text-figure 16.

Discussion: Two cranidia from locality 3 (Pl. 14, figs. 2, 3) are smaller (length (sag.) 0.46 and 0.57 mm.; maximum width 0.75 and 0.85 mm. respectively) than those previously described, though not as small as that of *C. triacantheis* (Whittington and Evitt, 1954, p. 60). They do not have fixigenal spines, but are larger than the cranidia with fixigenal spines of *Apianurus* n.gen. and *Diacanthaspis* described here, and thus seem to represent the immediately succeeding stage when these spines are lost. Notable is the convexity of the glabella of the smallest, on which there are axial pairs of spines 2, 3, and 4 (Text-fig. 16; equivalent

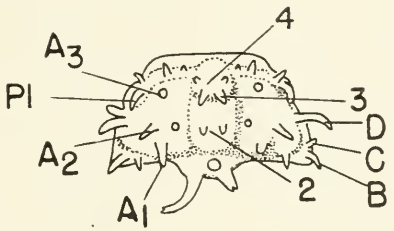


Figure 16. *Ceratocephala laciniata* Whittington and Evitt. Cranidium, exterior view, X 38. Drawn from the original of Plate 14, figure 3. Paired spines numbered and lettered as in Text-figure 1.

to 3, 4, and 5 of Whittington and Evitt, 1954, p. 61, fig. 16), the glabella being highest where spines 3 are situated. Lateral glabellar lobes cannot be distinguished. The palpebral lobe is far forward, bearing a long, curved spine (Pl in Text-fig. 16) and there are three spines on the eye ridge. On the convex fixed cheeks spines A_1, A_2, A_3, B, C, and D may be recognized, and between the spines on both glabella and cheeks there are tiny close-spaced spines. The larger of these two cranidia (Pl. 14, fig. 2) shows characters intermediate between the smaller and the originals of Whittington and Evitt (1954, Pl. 7, figs. 1-8). Pairs of spines 2a, 2, 3, 4, and 5 (equivalent to 2-6 of Whittington and Evitt, 1954, text-fig. 16) are now present on the fronto-median glabellar lobe, as well as a pair on the flanks between 2 and 3.

Basal lateral lobes are faintly developed, and bear a stout median spine, and with this inflation the fixed cheek no longer slopes inward to the axial furrow.

Additional and better-preserved hypostomes (Pl. 14, figs. 11, 12) have shown that the inner edge of the postero-lateral doublure is flexed upward, and just behind the lateral notch it is also thickened. This slight projection may be regarded as the posterior wing. The doublure is flexed (the flexure running almost transversely) at the shoulder, and on the anterior side of the flexure, near the outer edge, a hole pierces the doublure. This hole is present in small hypostomes, is variable in size and usually elongated transversely.

From localities 2, 3, and rarely 4, come the objects shown in Plate 14, figures 5, 6, 10, 13-15. They show a range in size and are both right and left-handed. The two divergent blade-like spines, with a row of thorn-like barbs, curved distally, along each side, are like the anterior thoracic pleural spines and the pygidial border spines of *C. laciniata.* As in these latter spines, there are openings at the tip of the barbs (Pl. 14, fig. 14). The fused base of the two spines is attached to a flat strip which resembles the outer part of a thoracic pleura of *C. laciniata;* it is without a "pleural" furrow, the transverse edge is flattened and bears a row of tiny tubercles along the "upper" edge. The anterior edge of the strip is also very like the anterior edge of the pygidial pleural region, notably in the way the flattened edge slopes forward at the "fulcral articulating process" (Pl. 14, figs. 8, 10). On the opposite ("ventral") side the end of the "pleura" is rolled under and there is an antero-lateral projection ("fulcral articulating process") and a "fulcral" socket beneath the fused base of the spines. When placed as in Plate 14, figures 4, 8, 9, between the outer part of a posterior thoracic segment and a pygidium, the resemblance of this object to the outer part of a pleura is extremely close. Further, the angle made by the lateral margin, and parallel inner margin, of the "doublure," with the sagittal line is a large one, larger than that of an obviously posterior (with backwardly directed posterior pleural spine) thoracic segment. This angle is such as to make the line of the inner edge of the "doublure" fit between that of the pygidium and of a posterior segment, as shown in Plate 14, figure 4. Thus this

object, if it is part of a thoracic pleura, belongs to the posterior thoracic segment. It is not crossed by a pleural furrow, but such furrows, though present in some posterior segments (Whittington and Evitt, 1954, Pl. 6, fig. 6), are extremely shallow and not seen in posterior segments in which the posterior pleural spine points inward and backward. When this object is arranged as in Plate 14, figures 4, 8, 9, it is thus difficult to think of it as anything but the outer part of the posterior thoracic segment. There are difficulties to be surmounted before accepting this conclusion, viz.:

(1) Most serious is the fact that the "pleura" of the object is of constant length and the inner termination is a V-shaped edge, the anterior limb of the "V" the longer, the edge bevelled (Pl. 14, figs. 13, 15). If this object is the distal portion of a segment, why is it terminated in this way, when all other distal parts of segments found are obviously broken (Pl. 14, fig. 4; see also Whittington and Evitt, 1954, Pl. 6, fig. 6)? The flattened edge is like that of the anterior and posterior edges, which would be the sutures between segments. Is the inner edge of this object also a suture? If so these sutures would run symmetrically on either side of an axial ring and innermost pleural parts, a peculiar situation seemingly unique among trilobites. No such median part of this supposed segment has been found.

(2) Why are the two "pleural spines" of the object similar to each other, and not of the distinct anterior and posterior types of all other known segments? The border spines of the pygidium are also of the thoracic anterior pleural spine type, and so, if the object is the outer part of the last segment, it also represents this posterior simplification of spine type.

I have examined two entire specimens of *C. verneuili* in the Museum of Comparative Zoology collections, but they show no peculiar last thoracic segment, and no such segment is illustrated by Barrande (1852, Pl. 38, figs. 5, 6). The objects discussed above occur in material in which *C. laciniata* is fairly abundant, and they also occur in the lower Lincolnshire limestone with *C. triacantheis* Whittington and Evitt, 1954. *C. rarispina* n.sp. is not abundant in the Oranda formation, and these objects have not been found at locality 8. Tentatively I regard these objects as part of a thoracic segment of *Ceratocephala*, but the various

problems mentioned above remain at present unsolved. If they are truly distal parts of the last thoracic segment, the reconstruction given by Whittington and Evitt (1954, fig. 13) requires modification on the lines suggested by Plate 14, figure 8.

Ceratocephala rarispina Whittington, n.sp.

Plate 15, figures 1-25, 28, 29.

Holotype: USNM 116527 (Pl. 15, figs. 1, 4, 5, 7), locality 8.
Other Material: Paratypes USNM 124698 a-d; all figured specimens in USNM.
Geological Horizon and Locality: Oranda formation, locality 8. This species is rare at locality 8, as shown by the following table:—

Table 3

Numbers of Odontopleurid Cranidia at Locality 8.

Diacanthaspis orandensis n.sp.	120
Diacanthaspis scitulus n.sp.	25
Diacanthaspis aff. *ulrichi* n.sp.	2
Apianurus barbatus n.gen., n.sp.	22
Ceratocephala rarispina n.sp.	7

Description: This species differs from both *Ceratocephala triacantheis* and *C. laciniata* (Whittington and Evitt, 1954, pp. 54-60, Pls. 6-9, 25, 26, figs. 1-17), bearing perhaps more resemblance to the former, older, species than the latter. Points of discrimination are:—

1) Occipital ring lacks posterior band, and paired spines are more strongly curved outward.

2) Third lateral glabellar lobes not developed.

3) First and second lateral glabellar lobes more inflated and separated from both median lobe and cheeks by well marked furrows.

4) Eye lobe situated farther back than in *C. laciniata.*

5) Border of free cheek subdivided by groove into two convex bands of about same width, both of which merge into base of librigenal spine.

6) Few, larger spines on external surface of cephalon. Six pairs on median glabellar lobe include 2a, 2, 3, 4, 5, the latter being far apart, and an additional pair far apart between 2 and 3. All have counterparts on other two species (e.g. compare Pl. 15, fig. 1, with Whittington and Evitt, 1954, Pl. 8, fig. 1; Pl. 25, fig. 10), as has swollen base of pair 3. Two spines on eye ridge rather than three. Spines along margin of free cheek longer. Conspicuous on *C. rarispina* are the tiny spines that line the edges of occipital furrow and furrows on cheeks (Pl. 15, figs. 1, 29).

7) Hypostome with shallower lateral notch and narrower postero-lateral border.

8) Pygidium with much shorter median border spine.

In *Ceratocephala laciniata* some of the thorn-like spines scattered over the glabella and cheeks appear to have a single opening at the tip (Whittington and Evitt, 1954, p. 59). In at least one specimen of *C. rarispina* (Pl. 15, fig. 28), however, some of these spines are covered over at the truncated tip, there being several minute depressions or openings in the plate covering the tip (appearing as darker spots in the photograph). This structure is like that in *Diacanthaspis* described above, and whether or not hairs emerged from the tips of these spines is uncertain.

Subgenus CERATOCEPHALINA Whittington, n.subgen.

Type Species: *Ceratocephala* (*Ceratocephalina*) *tridens* Whittington, n.subgen., n.sp.

Discussion: C. (*Ceratocephalina*) *tridens* displays many of the exoskeletal characters of *Ceratocephala* — the subtrapezoidal outline of the convex cephalon, broad, long (sag.) occipital ring, large basal, smaller second, and extremely small third lateral glabellar lobes, prominent eye ridge and eye lobe, and librigenal spine originating on the postero-lateral border of the free cheek; the thoracic pleurae are not furrowed and bear two pleural spines, the anterior shorter, with lateral barbs; the pygidium is short, triangular; paired axial spines are prominent on each segment, and the ornament is of large, well-spaced spines. Yet it is distinguished from any of the three species of *Ceratocephala*

in the Middle Ordovician of Virginia (and other species of this genus) by a well-marked group of characters: (1) the lesser inflation of the lobes (fronto-median and lateral) of the glabella: (2) the position of the large eye lobe, far back opposite the midpoint of the basal glabellar lobe, and the consequent alignment of the branches of the dorsal suture; (3) the prominent median occipital spine, as large as the paired spines; (4) the relatively longer pygidium, axis well-marked, and lacking the median border spine. The differences between *C. laciniata, C. triacantheis* (Whittington and Evitt, 1954) and *C. rarispina* n.sp., seem to be less than those between any one of them and *C.* (*C.*) *tridens*, and I have recognized these differences as of subgeneric rank. If the hypostome associated with *C.* (*C.*) *tridens* is correctly placed, the subsquare outline and well-defined subtriangular anterior lobe of the middle body afford further distinguishing characters of the subgenus.

Only the cephalon is known of *Whittingtonia bispinosa*, from the Upper Ordovician of Eire and Sweden (Text-fig. 17). It is distinguished from *Ceratocephala* (*Ceratocephalina*) by the far more prominent median glabellar lobe, the relatively narrow basal glabellar lobe, the more anterior position of the eye lobe, lack of median occipital spine, and less prominent ornament. *Proceratocephala* (Whittington, 1956b), also an Upper Ordovician genus, has more inflated median and lateral glabellar lobes, lacks the median occipital spine and has the paired spines differently situated, has well-marked pleural furrows in the thoracic segments, and a pygidium with more prominent border spines.

Ceratocephala (Ceratocephalina) tridens Whittington, n.subgen., n.sp.
Plate 16.

Holotype: USNM 124699 (Pl. 16, figs. 1-3, 18), locality 4.

Other Material: Paratypes USNM 124700 a-c, all figured specimens in USNM.

Geological Horizon and Locality: lower Edinburg limestone, localities 3 and 4.

Description: Outline and form of cephalon shown in Plate 16, figures 1-7. Occipital ring set off from posterior border by

change in slope and backward curve of posterior margin, longest (sag.) medially; occipital furrow deep only behind basal lateral glabellar lobes. Lobes of glabella gently convex, separated from each other by broad, shallow furrows, only the inner parts of the first and second glabellar furrows relatively deeper, and the third furrow represented by a subcircular pit behind the eye ridge (Pl. 16, figs. 3, 6); third glabellar lobe extremely small. Change of slope only separates glabellar from anterior border, axial furrows shallow beside first glabellar lobes, elsewhere glabella merges into cheeks. Eye lobe large, subspherical, situated on highest point of cheek, and opposite a point on midline just in front of occipital furrow. Palpebral lobe vertical, anteriorly merging with eye ridge, which curves forward to join with most anterior part of glabella. Eye surface (Pl. 16, figs. 23, 24), with each facet convex externally, concave internally. Anterior branch of suture curves forward, diverging slightly from eye ridge, crosses anterior border furrow on low sutural ridge, and turns abruptly to run inward and downward across anterior slope of border to meet rostral suture at obtuse angle. Rostral suture runs along outer edge of narrow (sag. and exs.) anterior border. Posterior branch of suture (Pl. 16, fig. 18) runs down the vertical cheek, in a curve convex outwards, and across posterior border furrow and border. Two branches of suture are approximately aligned and thus do not make an angle at eye lobe. Free cheek (Pl. 16, figs. 23, 24) with broad border occupying almost half the width at the librigenal spine, shallow border furrow, midpart of border, between rolled margin and inner part, concave upward. Librigenal spine arising inside edge of border, base merging into border, the low swelling extending forward especially conspicuous. Interior view (Pl. 16, figs. 6, 9) shows doublure widest laterally, and ridges formed by deepest parts of occipital and glabellar furrows. Rostrum must be short (sag. and exs.) but broad (tr.). Hypostome tentatively placed here (Pl. 16, figs. 19-22) sub-square in outline, middle body convex, divided by shallow furrows into sub-triangular anterior lobe and crescentic posterior lobe, well-marked depression in antero-lateral corner. Lateral notch extremely shallow, shoulder small, pointed, posterior border wide (exs.) with median notch. Major cephalic spines are librigenal and paired

and median occipital spines. The next size, thorn-like, include those on the major spines, those projecting from edge of lateral border, paired spines of glabellar lobes, palpebral lobe, eye ridge, free cheek, etc. Fine granular ornament extends over dorsal surface between these spines.

Number of thoracic segments unknown. Axis broad, pleura relatively narrow (tr.). Construction of axial rings and pleurae like *Ceratocephala* (cf. Whittington and Evitt, 1954, Pl. 8, figs. 8, 10), but appendiferal pits shallower and anterior pleural spines curved, directed outward and downward, not steeply downward as in *C. laciniata* and *C. triacantheis*. The posterior pleural spines are directed slightly upward and progressively more strongly backward, so that on a posterior thoracic segment (Pl. 16, fig. 12) they point almost directly back. The pair of spines on the axial ring are long and curve outwards. Thorn-like spines occur on them and on the pleural spines. Pygidium (Pl. 16, figs. 15-17) with axis undivided, but the two pairs of axial spines suggest it may be composed of at least two segments. Pleural regions without border, one major pair of spines arising behind axis on upper surface, directed backward and upward; doublure narrow with broader (sag.) "tongue" projecting toward axis. Many short spines on edge of border, smaller spines on pleural lobes.

Discussion: From locality 4, where most of the specimens of *C.* (*C.*) *tridens* have been found, comes a single small cranidium of the same general type, but displaying certain differences (Pl. 15, figs. 26, 27, 30). Most striking are the long curving pair of occipital spines, the bases closer together, and the small median occipital spine. The external surface is covered with tiny tubercles, and the spines in the row on the fixed cheek are longer than those of *C.* (*C.*) *tridens*. The different appearance of the external surface of this cranidium may be the result of preservation, but the difference in the occipital spines is suggestive of a specific difference. Perhaps this cranidium represents a second species of *Ceratocephala* (*Ceratocephalina*).

Genus PROCERATOCEPHALA Prantl and Přibyl, 1949
Synonym: *Drummuckaspis* Prantl and Přibyl, 1949
Type Species: *Acidaspis terribilis* Reed, 1914.

Discussion: The type species has been described in detail elsewhere (Whittington, 1956b), and is like *Ceratocephala,* but differs in the presence of long paired spines and lateral lobes on axial and occipital rings, possessing 9 thoracic segments with deep pleural furrows, and a pygidium with a long major and short median border spine. The cephalon displays some features recalling *Miraspis,* but is too poorly known to allow detailed distinctions to be made. *P. terribilis* is known only from the Upper Ordovician of Scotland.

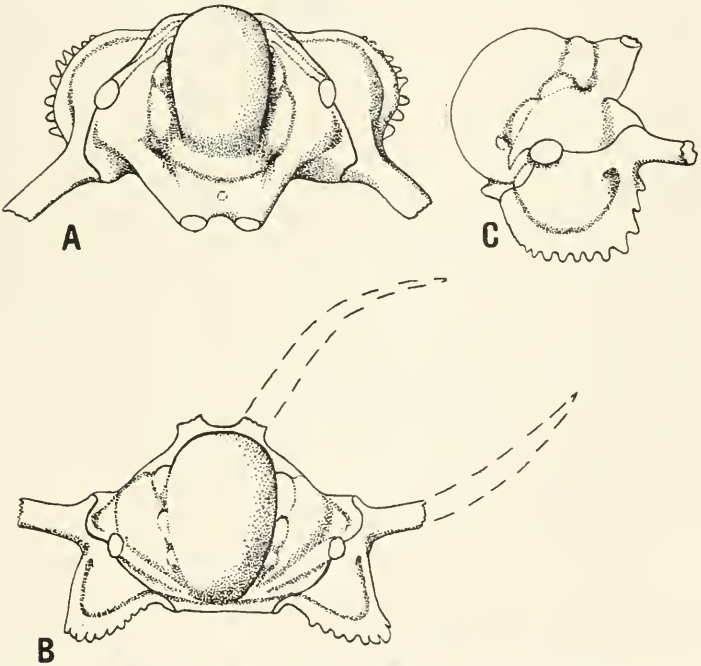


Figure 17. *Whittingtonia bispinosa* (M'Coy), Upper Ordovician, Chair of Kildare, Eire. A, B, C, incomplete cephalon, exterior, anterior, and left lateral views, approximately X 3. Drawn from originals of Whittington 1956b, Plate 59, figures 4, 5, 7, 8.

Genus WHITTINGTONIA Prantl and Přibyl, 1949

Text-figure 17.

Type Species: *Acidaspis bispinosus* M'Coy, 1846.

Discussion: Only the cephalon is known, and a well-preserved specimen has recently been described (Whittington, 1956b). It is distinguished from *Ceratocephala* by the three narrow (tr.) pairs of lateral lobes and wide (tr.), strongly convex fronto-median lobe which overhangs the anterior border and has a convex band across the base, and the short, thick spines on the lateral cephalic border. Specimens are known from the Upper Ordovician of Eire and Sweden.

Genus DICRANURUS Conrad, 1841

Text-figure 18.

Type Species: *Acidaspis hamata* Hall, 1859 (Whittington, 1956b).

Diagnosis: Occipital ring without posterior band, paired spines thick and long, recurved in a hook extending over the thorax. Small third lateral glabellar lobes. Eye lobe situated opposite basal glabellar lobe on highest part of convex cheek. No spines on lateral cephalic border. Nine thoracic segments; anterior pleural spine blade-like, with lateral barbs, curved downward and backward; convex posterior pleural band continued into stout posterior pleural spine, anterior directed outward, remainder outward and backward. Pygidium with pair major border spines only, connected by strong pleural ridge to first axial ring.

Geological Range: Lower to Middle Devonian.

Notes on Other Miraspinid Genera

Selenopeltoides Prantl and Přibyl, 1949, type species by original designation *Acidaspis hawlei* Barrande, 1852, from the

Figure 18. *Dicranurus monstrosus* (Barrande), Prokop limestones, $g\alpha_2$, Middle Devonian, Lochkov, Bohemia. A, anterior view of cephalon, B, C, dorsal and right lateral views of entire exoskeleton, approximately X 1½. After Whittington 1956b, text-figure 4.

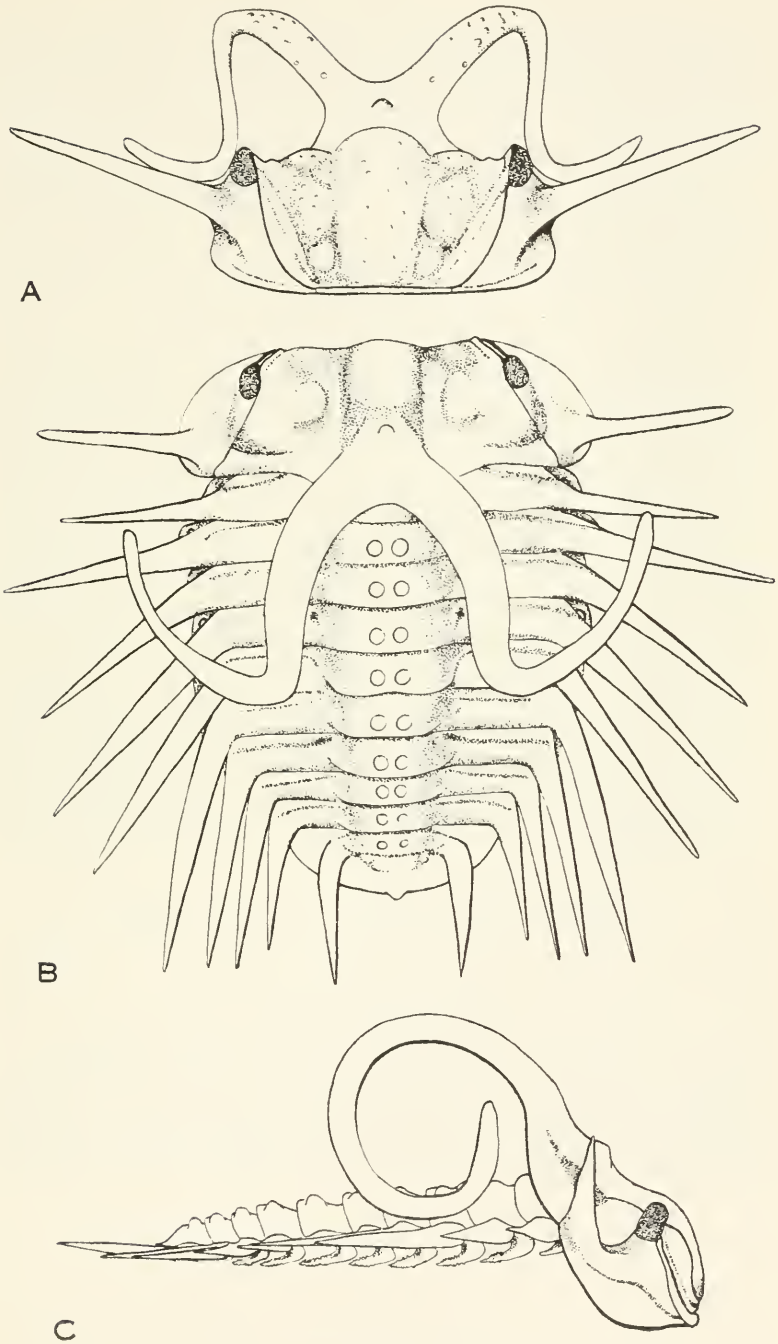


Figure 18

upper Middle Silurian of Bohemia. No material other than the original incomplete holotype (and an isolated pygidium, now missing) is known, so that the basis for a genus is most unsatisfactory. Erben (1952b) suggested that the type species was most closely related to *Dicranurus*, which appears probable.

Orphanaspis Prantl and Přibyl, 1949, type species by original designation *Trilobites orphanus* Barrande, 1852, Middle Silurian. Beside the type species, two others have been recognized in the Lower and early Middle Devonian of Germany (Erben, 1952a, pp. 306-308, 314-316, text-figs. 52, 54, Pl. 20, figs. 7, 13; 1952b), but all are based on pygidia only, of miraspinid type.

Koněprusia Prantl and Přibyl, 1949, type species by original designation *Acidaspis fuscina* Novák, 1883, lower Middle Devonian. Three species originally described by Barrande were placed in this genus by Prantl and Přibyl (1949, pp. 199-202), but of neither the type species nor these other species was new material described or new figures given. The pygidium of the type species is distinctive, the border spines being only one stout pair and a median posterior, but the cephalon is poorly known. Tentatively this material may be recognized as representing a separate genus, presumably of miraspinid type, but until it is better known its position will remain uncertain.

Ceratonurus Prantl and Přibyl, 1949, type species by original designation *Acidaspis krejčii* Novák, 1883. I have no new observations to add to those of recent authors (Prantl and Přibyl, 1949, pp. 189-192; Erben, 1952a, pp. 308-313; Erben 1952b), and all are agreed that this Lower and Middle Devonian genus is of *Ceratocephala* type. It may be derived from this latter genus or from *Miraspis*.

?Subfamily MIRASPINAE R. and E. Richter

Odontopleurid Protaspis

Plate 21, figures 23, 24.

Material: USNM, one incomplete specimen from locality 4.

Discussion: This specimen is smaller than either of the protaspides of *Diacanthaspis lepidus* n.sp. (Pl. 4, figs. 1-5) and *D. secretus* n.sp. (Pl. 6, figs. 1-5) from the same locality, but is of extremely similar form. It differs principally in that the fixi-

genal spine and those on the external surface are slimmer and less swollen at the base. On the parallel-sided glabella only the thick median occipital and axial spine pair 3 are present. On the cheek, which is most convex in the inner part, the fixigenal and spines A_1, A_2, A_3, B, C (directed almost straight outward and somewhat upward), D (about midway between C and palpebral lobe), Pl and Er may be seen, and there is an additional spine about midway between A_2 and B. The protopygidium has a markedly triangular outline, convex axis bearing two pairs of spines, two pairs of spines on borders, at base of anterior of which is short upwardly-directed spine.

The presence of only spine pair 3 on the glabella and the outline of the protopygidium, as well as the slimmer spines on the external surface, make it unlikely that this protaspis is that of *D. lepidus* or *D. secretus*. The Stage 0 cranidium of *D. ulrichi* n.sp. (Pl. 8, fig. 10), has stout fixigenal and median occipital spines, but others are faint, and the outline also is unlike that of the cranidium of this protaspis. The Stage 0 cranidium of *Apianurus barbatus* n.gen., n.sp. (Pl. 19, fig. 2), has stouter spines, including paired occipital, pairs 2 and 4, and those of the anterior border, all of which distinguish it. Thus I am driven to suggest that this protaspis might be that of *Ceratocephala laciniata*, which is fairly abundant at this locality, but cannot exclude the possibility that it is that of the rare *C.* (*Ceratocephalina*) *tridens*, n.subgen., n.sp. No evidence can be offered for or against this latter possibility, since tiny cranidia of *C.* (*C.*) *tridens* are not known. The smallest known cranidia of *C. laciniata* (Pl. 14, figs. 2, 3) have an outline like that of the protaspis, notably the curve of the lateral sutural margin, anterior border without spines, eye lobe far forward, fixed cheeks lacking fixigenal spine but having all lettered spines and some additional. The glabella of these small *C. laciniata* cranidia, however, is strongly convex, spine pair 3 most prominent, but long, curved paired occipital spines are present as well as pairs 2 and 4, and the median occipital spine is small. It is chiefly this difference in the glabellae that makes me hesitate to identify this protaspis as that of *C. laciniata*, though there are also differences in the disposition of the lettered spines on the fixed cheek. Only the discovery of cranidia intermediate between this

protaspis and the smallest of *C. laciniata* would show how, if they belong to the same species, the transition takes place.

Subfamily APIANURINAE Whittington, n.subfam.

Diagnosis: Glabella narrows forward, occipital ring long (sag.), convex, long paired spines and median tubercle; well defined, parallel-sided median lobe, two pairs of lateral lobes fused. Eye lobe situated far back and about midway across cheek, two branches of suture forming a straight line inclined inward and forward to the sagittal line, free cheek narrow, librigenal spine arising about midway along lateral border and curving back. Hypostome shield-shaped, middle furrow arises at antero-lateral corner of middle body and runs inward and backward; small, pointed shoulders and shallow lateral notch. Thorax of unknown number of segments, pleurae convex (exs.), single large pleural spine. Pygidium with paired border spines, unpaired median border spine may be present, long major spine upwardly directed.

Geological Range: Middle to Upper Ordovician.

Genus APIANURUS Whittington, n.gen.

Type Species: *Apianurus barbatus* Whittington, n.gen., n.sp.

Diagnosis: Long occipital spines diverge at 60-80°; fused lateral lobes kidney-shaped. Large eye lobe opposite basal glabellar lobe. Hypostome widest anteriorly, convex middle body divided into triangular anterior and crescentic posterior lobe; small anterior, tiny posterior, wings. Pygidium with six or seven pairs border spines, flat pleural region bearing centrally-situated upright major spine. Long spines (except occipital) with thorn-like lateral spines, remainder of exoskeleton tuberculate or spinose.

Geological Range: Middle and Upper Ordovician. An incomplete cranidium and fragmentary free cheeks and thoracic segments testify to the presence of a species of this genus in the Lincolnshire limestone, below the Edinburg limestone.

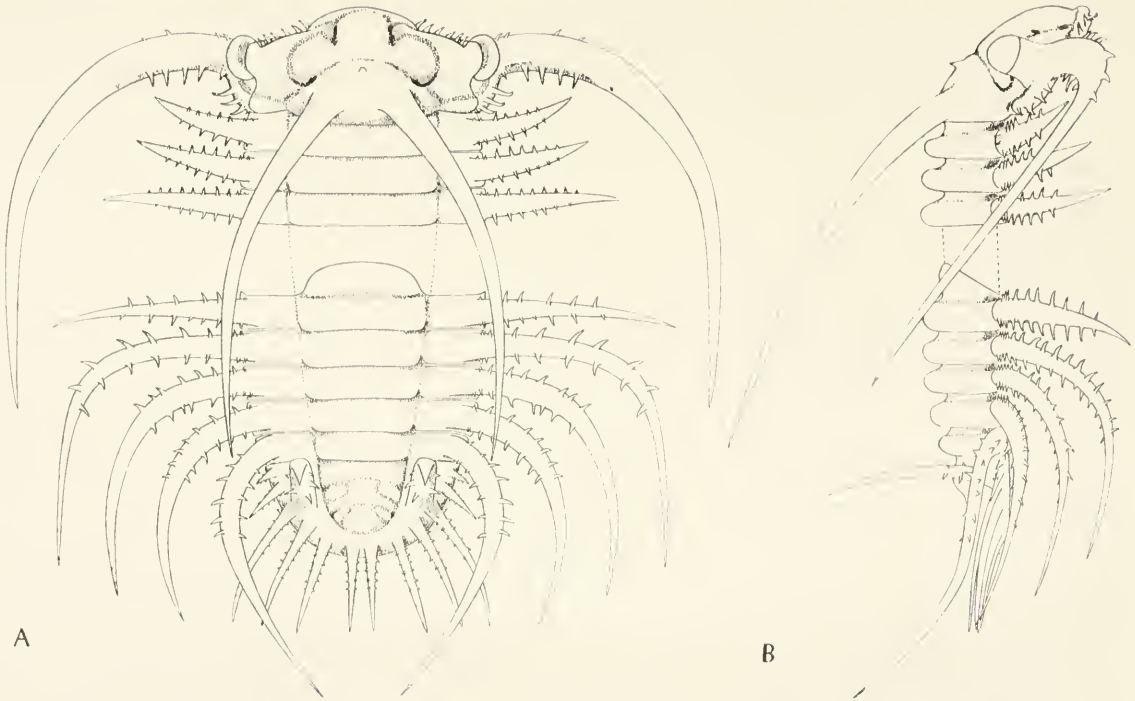


Figure 19. *Apianurus barbatus* n.gen., n.sp. Reconstruction, A, dorsal, B, right lateral views. Number of thoracic segments unknown. Approximately X 4.

APIANURUS BARBATUS Whittington, n.gen., n.sp.

Plates 17-19; 20, figures 1-17, 19; Text-figures 19-22

Holotype: USNM 124701 (Pl. 17, figs. 3, 4, 6), locality 2.
Other Material: Paratypes, USNM 124702 a-e; all figured specimens in USNM.
Geological Horizon and Localities: Edinburg limestone, localities 2, 3, 4, 6, 8.

Description: Cephalon moderately convex, outline in dorsal and anterior aspect elliptical. Glabella moderately convex transversely, gently convex longitudinally, maximum width across occipital ring, narrowing forward to half this width at anterior margin; length about two-thirds maximum width. Occipital ring of length (sag.) in dorsal aspect half that of rest of glabella, becoming narrower (exs.) laterally, outline of posterior margin a curve strongly convex posteriorly, outline of anterior margin a curve more gently convex anteriorly. Stout occipital spines diverge at about 60° and curve upward and backward, extending to a length three times the sagittal length of the cephalon. Small median occipital spine just behind occipital furrow. Latter shallow medially, deep behind basal lateral lobes. First and second glabellar lobes fused to give a kidney shape, the second the smaller, the first glabellar furrow represented by a subcircular pit adjacent to the median lobe. A pit anterior to the second glabellar lobe represents the second glabellar furrow, and is bounded anteriorly by the eye ridge as it fuses with the frontal glabellar lobe. Outline of anterior margin of latter curve convex forward, and separated by change of slope from narrow anterior border. Fronto-median lobe gently convex, change of slope separating it from lateral lobes, faint additional swelling running transversely across it between first glabellar lobes. Axial furrow not deep, but a narrow, unornamented band, marking reversal of slope between cheek and glabella. Cheek semicircular in outline, maximum width opposite second glabellar lobe, rising steeply to large eye lobe. Transverse line through mid-point of eye lobe passes through mid-point of first glabellar lobe and runs just in front of occipital furrow. Anterior branch of facial suture runs straight forward and inward at about 45° to the midline, curving inward a little more as it

crosses the border on a sutural ridge. Posterior branch runs out and back in line with anterior branch for a short way, then curves in over posterior border. Latter longest (exs.) at suture, convex, and becomes shorter inward. Thus the occipital ring merges with inner corner of cheek rather than with posterior border. Fixed cheek slopes vertically behind eye lobe. Palpebral lobe with rim becoming well-defined anteriorly, and passing into broad, convex eye-ridge. Latter runs with a slight curve inward and forward to merge with frontal glabellar lobe. Eye surface almost hemispherical, external surface (Pl. 17, fig. 21) showing faintly the tiny facets. Lateral cephalic border rolled, shallow border furrow interrupted at about mid-length by swelling at the base of librigenal spine. Latter directed outward and slightly forward at first, then curving and slimming to point backward, and reach to a length about three times that of the cephalon (sag.). Just outside anterior branch of suture is antennular notch (Pl. 17, fig. 5), with a sharp projection at outer margin. Anterior border between sutures narrow (sag. and exs.), rostral suture running along outer edge. Rostrum unknown, but presumably wide (tr.) and short, sloping downward and inward. Doublure narrow on free cheek, absent on posterior border of cranidium, articulating half-ring long (sag.). On inner surface of cranidium (Pl. 17, fig. 12) outer part of occipital ring, first and second glabellar furrows make rounded projections but are not extended as appendifers. Width of hypostome (Pl. 18, figs. 1-5) at anterior margin greater than length, rounded postero-lateral outline, faint median posterior notch. Anterior wing small, tip rounded, no wing process. Lateral border narrow, gently convex, deep border furrow, shallow lateral notch and sharply-pointed shoulder. Posterior border wider and in median portion separated by shallow depression from median body. Outermost part of posterior border bent up sharply near midline. From the broad depression at antero-lateral corner the middle furrow runs straight inward and backward to define triangular, convex anterior lobe of the middle body. Posterior lobe crescentic in outline, inflated. Doublure of hypostome widest laterally, disappearing at anterior wing and pressed close to median part of posterior border so that edge is sharp. Ridge crosses doublure from point of shoulder to inner edge, immediately behind ridge doublure extended inward to form small tri-

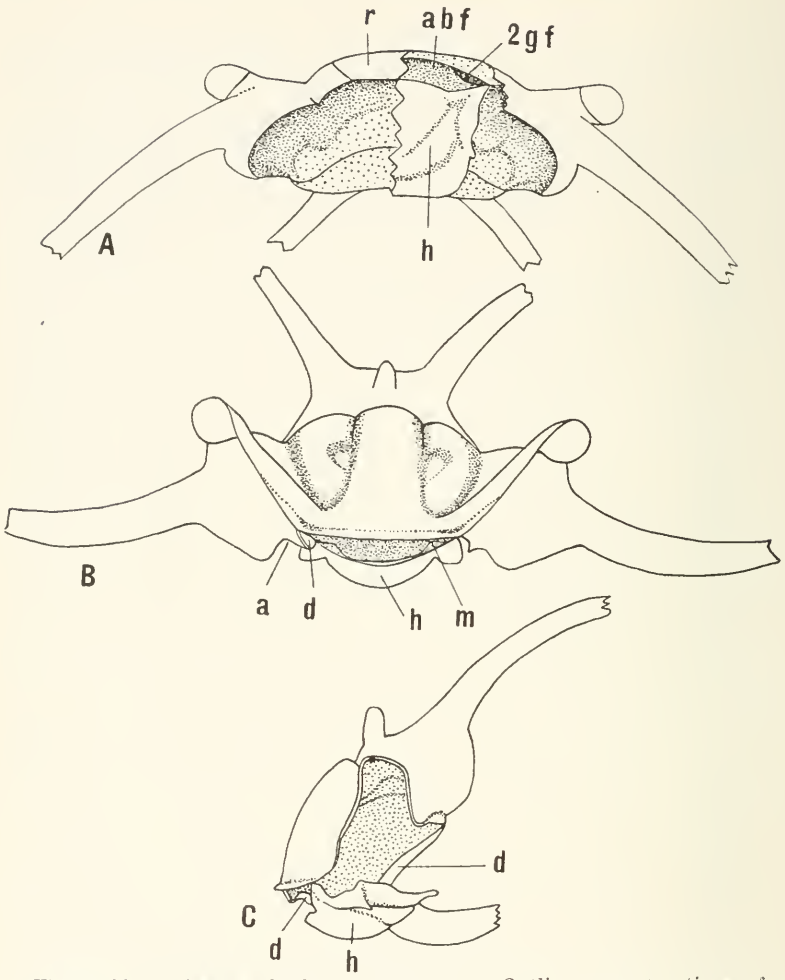


Figure 20. *Apianurus barbatus* n.gen., n.sp. Outline reconstructions of cephalon, approximately X 10. A, ventral view, right half of rostrum and left half of hypostome shown, anterior portion of left free cheek incomplete. B, anterior view, rostrum not shown and anterior portion of left free cheek incomplete. C, left lateral view, rostrum and left free cheek not shown. a, antennular notch; abf, ridge on inner surface corresponding to anterior border furrow; d, doublure of right free cheek; 2gf, ridge on inner surface corresponding to second glabellar furrow; h, hypostome; m, boss corresponding to depression at outer end of middle furrow; r, rostrum.

angular posterior wing. Perforation through doublure posterior to ridge (Pl. 17, fig. 19).

By mounting a cranidium and free cheek of appropriate size in juxtaposition, as shown in Plate 17, figures 5, 7, 9-11, the approximate position and attitude of the hypostome has been determined (Text-fig. 20). The gently-curved hypostomal suture (Pl. 18, figs. 1, 5) fits against the rostrum, and the anterior wing is directed upward and outward, the tip lying beneath the deepened outer part of the anterior border furrow where it meets the furrow bounding the outer side of the eye ridge. There may have been muscles linking the wing and inner side of the furrow, but there is no wing process or socket. The depression at the outer end of the middle furrow forms a considerable projection on the inner surface (Pl. 18, fig. 2), and may have been a point of muscle attachment. Perhaps it was linked by muscles to the outer end of the anterior border furrow. The shape of the rostrum is suggested, and is consistent with the form of the few odontopleurid rostra known (Whittington, 1956b, Pl. 58, fig. 7; Pl. 59, fig. 3). If the cephalon rests on a flat surface on the antero-lateral cephalic border and librigenal spines, as portrayed in Text-figure 20 B, C, the middle body of the horizontal hypostome would lie on this surface.

Ornament of cephalon of close-spaced spines which curve characteristically toward the closed tip (Pl. 17, fig. 21; Pl. 18, fig. 22). The spines vary in size, the exoskeleton between their bases smooth, as are also the axial, occipital, and glabellar furrows. Arrangement of spines not perfectly regular, but symmetrical pairs of larger spines may be distinguished even on largest cranidia, on the occipital ring, median and lateral glabellar lobes, eye ridge, etc. (Pl. 17, fig. 2). Single row of symmetrical spines on anterior border of cranidium. Large, curved spines are also regularly arranged on the border of the free cheek and the proximal portion of the librigenal spine (Pl. 17, figs. 1, 7, 14, 15) — e.g. four long and one short spine on the border behind the librigenal spine; stout spine at edge of antennular notch, one of same size midway to base of librigenal spine; 6 spines along outer side of proximal part of librigenal spine, etc. The characteristic curved spines are not present on the distal part of the librigenal spine, nor on the occipital spines. Much shorter, blunt,

spines are present, directed outwards on the proximal portion of the spine, but distally inclining more and more in the direction of the main spine, so that at the tip they lie at a low angle to the surface (Pl. 17, fig. 3). Toward the tip of the main spine, on the distal side of the base of the small spine, a minute opening is sometimes seen — apparently the locus of a sensory hair. Other cephalic spines do not seem to show such openings. Proximally, in the region where there are the large lateral spines, the under side of the librigenal spine is smooth, as is the doublure of the free cheek. The characteristic curved spines occur on the lateral and posterolateral borders of the hypostome (Pl. 18, fig. 1), but are reduced to granules on the posterior border. Similar spines are scattered on the lateral areas of the middle body, but the central portion is smooth.

Number of thoracic segments unknown. A sufficient number of the delicate segments are preserved to permit the reconstruction (Text-fig. 19 A, B), which is based on the assumption of a total of ten. Axis broad, two-thirds total width (excluding pleural spines) at anterior segment (Pl. 18, fig. 6), narrowing back to half its width at posterior segment (Pl. 18, fig. 9). Axial ring moderately convex, posterior margin forms a curve, convex posteriorly. Articulating furrow more strongly curved in same sense, outermost part deepened. Articulating half-ring longer (sag.) than axial ring. Pleura narrowest (tr.) in anterior segments, horizontally extended, without pleural furrow. Narrow (exs.) flanges developed, outer surface of each flat and inward and downward sloping. Ring and axial articulating sockets and processes scarcely at all developed, but lateral margin of pleura rolled under and fulcral socket and process prominent. Base of pleural spine swells out from upper, outer surface of pleura. Length, curvature and direction of pleural spines indicated in reconstruction. The characteristic curved ornamental spines are close together on the axial ring, varying in size, some larger ones paired. Similar spines more widely scattered on pleurae. Pleural spines ornamented like librigenal, with row of lateral, curving hooks on each side of proximal part, and the tiny inclined spines distally (Pl. 18, fig. 9). Similar openings to those on the tips of the occipital and librigenal spines seem to be present.

Pygidium (Pl. 18, figs. 11-13) semi-oval in outline, length

(sag.) a little more than one-third width at anterior margin. Axis moderately convex, a little wider than long, rounded posteriorly, rising from the flat pleural regions and not defined by deep furrows. Articulating furrow and half-ring like those of segments. First ring furrow broad and deep, curving forward to midline, extremities widened and deepened. Second ring

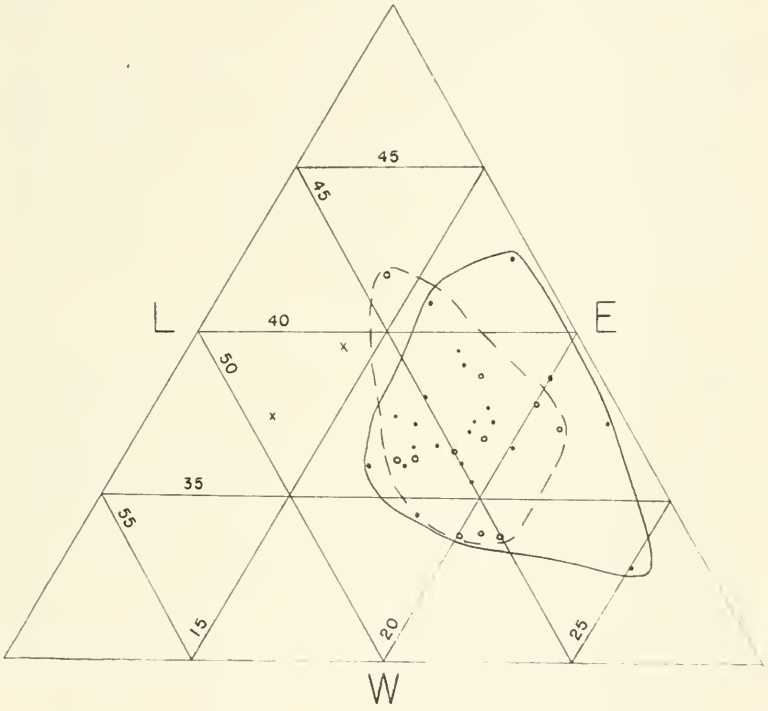


Figure 21. Triangular graph comparing relative proportions of dimensions of cranidia of *Apianurus barbatus* n.gen., n.sp. Those from the lower Edinburg formation, localities 2, 3, shown by dots enclosed by solid line. Cranidia from the Oranda formation, locality 8, shown by open circles enclosed by broken line. Two tiny cranidia from locality 3 shown by X (originals of Plate 19, figures 2, 9). L, sagittal length of cranidium. W, width between spines B on posterior border. E, length (exs.) from anterior margin to midpoint of palpebral lobe. Measurements were made in exterior view, i.e. with isolated cranidium resting on a horizontal surface.

furrow represented only by pair of oval, unornamented areas on terminal part of axis, corresponding in position to wider outer part of first furrow. In many specimens these two pairs of oval areas are translucent, the quartz much thinner over them, or broken, indicating that they may be areas of muscle attachment (cf. Whittington and Evitt, 1954, pp. 24-25). Long spine rises vertically from flat pleural region, opposite first ring furrow, and distally curves a little backward. Border of pleural regions with 6 pairs of spines directed outward and slightly upward, first pair short, second longer, third longest, and remaining pairs shorter inwards. Doublure of pygidium narrow, rolled under at antero-lateral corner forming articulating process. Ornament of curved spines on pygidium (Pl. 18, figs. 12, 13, 19) disposed as on thorax — dense, varying in size, and with some conspicuous pairs on the axis, more widely spaced on pleural regions. Upright and border spines with lateral barbs, and towards tips the tiny inclined spines are present, and the openings may be present.

Discussion: In addition to the material from the lower Edinburg formation (localities 2, 3, 4; Pls. 17-19), that from the Oranda formation (locality 8; Pl. 20, figs. 1-17, 19) also represents *Apianurus barbatus*. Comparison of parts of the exoskeletons from all localities reveals no consistent differences between them. Measurements of length and width of cranidia and of position of palpebral lobe in specimens from both horizons fall within almost the same area of a triangular graph (Text-fig. 21). Locality 8 in the Oranda formation is some 450 ± feet higher in the section than localities 2-4 in the lower Edinburg, so that *A. barbatus* evidently has a long range in time. A few specimens (see Table 4) are known from locality 6, at an intermediate point in the section.

Figure 22. *Apianurus barbatus*, n.gen., n. sp. A, Stage 0 exoskeleton, dorsal view, drawn from originals of Plate 19, figures 1, 2, 5. Approximately X 32. B, cranidium, exterior view, drawn from original of Plate 19, figure 9. Approximately X 32. C, cranidium and right free cheek, exterior view, drawn from originals of Plate 19, figures 7, 8. Approximately X 32. D, cranidium and right free cheek, exterior view, free cheek from original of Plate 19, figure 11. Approximately X 32. E, cranidium, exterior view. Approximately X 32. F, cranidium, exterior view. Approximately X 16.

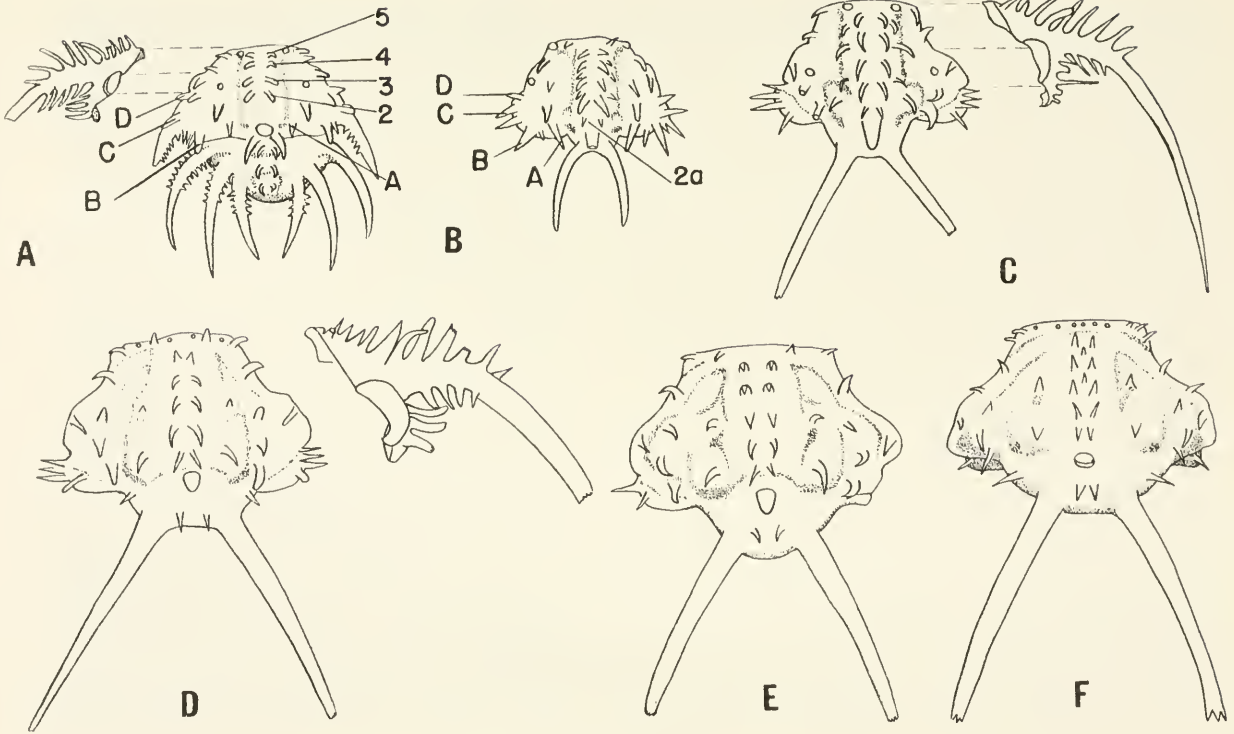


Figure 22

Development. Stage 0: Protaspis unknown, but the smallest known cranidium, free cheek and pygidium from localities 3 and 4 (Pl. 19, figs. 1, 2, 5) have been associated (by analogy with *Diacanthaspis*) to show the probable nature of the Stage 0 exoskeleton (Text-fig. 22A). Outline of cranidium (length (sag.) 0.41 mm.) trapezoidal, gently convex longitudinally, more gently transversely. Glabella outlined by broad, straight, axial furrows, short (sag. and exs.) occipital ring with prominent median and short curved pair spines, occipital furrow defined only distally, remainder of glabella without furrows, four prominent pairs short, curved, axial spines (2-5 in Text-fig. 22A). Narrow anterior border, fixed cheeks gently convex, palpebral lobes at two-fifths cranidial length (exs.) from anterior margin. Posterior margin of fixed cheek runs directly outward from the axial furrow, and just beyond half the width bends abruptly to run outward and forward to the base of the long fixigenal spine. On the outer, postero-lateral area of the fixed cheek there are 4 paired spines (A, B, C, D in Text-fig. 22A), and tiny spines along the inner side of the fixigenal spine and adjacent outer part of the fixed cheek. Certain specimens (Pl. 19, figs. 4, 6) have the fixigenal spine retained on one side only. Their significance is discussed under "Ontogeny" in Part I. Free cheek of appropriate size to fit this smallest cranidium (Pl. 19, figs. 1, 3; Text-fig. 22A) narrow, large eye surface situated at half length, big librigenal spine curving outward and backward. Anterior branch of the suture straight, posterior runs in curve convex outward, doublure projecting inward and fitting against doublure at base of fixigenal spine. Notch in anterior border outside suture very small. Long spines arranged in a constant pattern along outer edge of border and proximal edges of librigenal spine — conspicuous is variation in size of those along antero-lateral edge, curved spine at anterior basal edge of librigenal spine, numbers, curvature and/or inclination of remainder. Transitory pygidium of width at anterior margin 0.51 mm., length (sag.) 0.30 mm. Prominent axis bearing three pairs of curved spines, first two rings distinct, tip indistinct where posterior part of pygidium is bent sharply down. Pleural regions flat, borders bent down, 3 border spines arise on dorsal surface inside border, curving outward and backward. Doublure rolled under. Small barbs along sides of these border spines.

Further development of cephalon: Next largest cranidia (Pl. 19, figs. 9, 10; Text-fig. 22B) from localities 3 and 4 only. Parallel-sided glabella more convex, defined by deep axial furrows, tiny fifth pair of axial spines (2a in Text-fig. 22B) present just in front of occipital furrow Small lateral pairs of spines also present outside pairs 2, 3, and 4. Extremity of occipital furrow a shallow pit, in front of which is small swelling representing the beginning of basal glabellar lobe. Large palpebral lobe situated at about the same position. Most striking is the absence of fixigenal spine and rounded outline of genal angle of fixed cheek. Paired spines A, B, C and D (Text-fig. 22B) are developed as in the smaller cranidium, and there are one or two additional spines at the genal angle between B and C, as well as a small one on the fixed cheek between A and B. Free cheek associated with this size of cranidium very like that of Stage 0, but has eye surface situated behind mid-length, posterior branch of suture running in curve convex outward and seemingly little or not at all modified despite absence of fixigenal spine. Notch in anterior border is wider, spines along margins and proximal part of librigenal spine similar in size and arrangement to those on the smaller cheek.

The next largest cephala (Pl. 19, figs. 7, 8; Text-fig. 22C) show a marked increase in convexity of glabella and cheeks and in height of eye lobes. Occipital ring projects back farther behind cheeks, and paired spines now reach back to a length equal to that of cranidium. Midpoint of eye lobes is at about half the length, cheeks slope steeply behind them to border furrow, which runs out to margin between spines A and B. Eye ridge faintly defined. Median occipital and five paired spines of glabella prominent, additional lateral pairs developed, including 2 pairs (one central and one just in front) on convex basal glabellar lobe. On cheek and borders main spines developed as before but additional pairs also present. Next largest cephalon (Pl. 19, figs. 11, 14-16; Text-fig. 22D) similar, eye lobes at about same position, eye ridge more clearly defined. Occipital ring with longer paired spines, and relatively reduced median spine. In front of pits at extremity of occipital furrow are convex, ovate, basal glabellar lobes. In front of these, in line with anterior part of eye lobe and at base of side of glabella, a prominent pair of

spines. In slightly larger cranidia (Pl. 19, figs. 18-20, 22, 23; Text-fig. 22E) the area around the base of these spines is slightly swollen, and represents the second glabellar lobes. A deep pit represents the first glabellar furrow, and a faint swelling outside it connects the two lobes. Thus the bean-shaped fused lateral lobes are present at this stage, and become more prominent as the cranidium increases in size, swelling up to partly fill the depression between eye lobes and glabella. Other changes as size increases include appearance of swelling on median glabellar lobe just in front of occipital furrow, backward movement of eye lobes with consequent steeper slope behind them, and increased prominence of eye ridges. Many more ornamental spines appear, mostly paired, and a median row on the median glabellar lobe. The relative size of these spines diminishes, but even in the largest cranidia (Pl. 17, figs. 2, 3) the numbered and lettered pairs may be recognized by their slightly larger size, and most spines retain the characteristic curve so prominent in tiny specimens. The chief change in the free cheek from the size shown in Text-figure 22A is the backward movement of the eye lobe, so that the postero-lateral slope behind it is steep or overhanging. The arrangement of the spines on the border and proximal part of the librigenal spine remains basically the same, though the curved spine at the anterior basal edge of the librigenal spine is reduced, and an additional large spine (making six in all) appears along the anterior proximal margin of the librigenal spine. The margin of the antennular notch remains smooth, but the outer edge bears a large spine. Because the broad, swollen base of the librigenal spine merges into the cheek a border becomes defined by a shallow border furrow only near the branches of the suture.

Smallest known hypostome (Pl. 19, figs. 12, 13) 0.4 mm. in length (sag.), 0.55 mm. in width across anterior wings, proportions of various parts similar to adult. There is little change with increasing size.

Thorax and pygidium. Next largest transitory pygidium (Pl. 19, fig. 24) to that assigned to Stage 0 (Pl. 19, fig. 5) has three pairs of spines on the axis, 3 pairs long border spines, with lateral barbs, similarly directed to those of the earlier stage. An upright spine at the base of the anterior two border spines. Larger transitory pygidia (Pl. 19, figs. 25, 27-29) have four

pairs axial spines and four pairs border spines, the fourth border pair short, blunt, situated at tip. Latter less steeply bent down. First three border spines with lateral barbs and upright spine at base, direction and curvature shows slight variation, perhaps associated with stage. Latest transitory pygidium (Pl. 19, fig. 26) of length (sag.) 0.36 mm., width 0.7 mm. with 4 pairs of axial spines, posterior two close together at termination. Long, curved spines arising from the antero-lateral portions of pleural regions are pleural spines of what is to become last thoracic segment. Bases of broken-off pair of upright spines on pleural regions are opposite 3rd and 4th axial spines. Four pairs of border spines, third pair larger than others. Posterior tip of this pygidium not bent down. Small true pygidium (Pl. 18, figs. 23, 24) has first axial ring defined, with its pair of axial spines, and posterior part of axis bears two pairs of axial spines (and presumably therefore includes at least 2 segments). Swollen base of upright spine on the pleural region is connected with first axial ring. Margin with tiny anterior pair of spines and 4 larger pairs, third of these distinctly longer. As size increases (Pl. 18, figs. 16-18, 20, 21) the adult appearance is attained, except that there are still only 5 pairs of marginal spines, the anterior short, the others becoming equal in size. There are three pairs of axial spines, and a median spine on the tip of the axis. Large pygidia (Pl. 18, figs. 11-13) have six pairs of marginal spines, the first much shorter and slimmer than the rest. Behind the ring furrow the axis includes two pairs of axial spines, and a median spine at the tip.

Specimens from Localities 2 and 3

Differing from *Apianurus barbatus* n.gen., n.sp.

Under this heading may be grouped the following:

(a) Cephala and pygidia from both localities which are so strikingly different as to be regarded as representing a species of a distinct genus, described below as *Calipernurus insolitus* n. gen., n. sp.

(b) Cranidia from locality 2 which are like *A. barbatus* but are smoother — i.e. the spines are short, reduced to tubercles, or absent. These are described below as *A. glaber* n.sp.

(c) Pygidia occurring at both localities, distinguished from *A. barbatus* by being smoother and having shorter, inwardly-curved upright spines. These are here regarded as belonging with cranidia (b).

(d) A second type of pygidium occurring at locality 2, having the typical curved spine ornament of *A. barbatus*, but the upright spines are very short, and there are 7 pairs of spines on the border. This pygidium is described as *Apianurus* sp.ind.

(e) Three types of hypostome from locality 2, each different from that of *A. barbatus*. The one differing most has been assigned to *Calipernurus insolitus* n.gen., n.sp., the smooth one to *A. glaber* n.sp., the third described under "*Apianurus* sp. ind."

Each of the groups of specimens included under (a) to (e) is distinct, and there is no gradation between groups or between any one of them and *A. barbatus*. Within each group except (e) there are specimens of different sizes, showing that the distinctive characters of the group are not those of one particular size (i.e. growth stage). Table 4 shows the relative abundance of the different species at the different localities. Only *A. barbatus* is found in strata above the lower Edinburg. If the specimens grouped under (b), (c), and (d) were expressions of the morphological range of variation of *A. barbatus* one might expect them to be represented in the sample from locality 8. The fact that they are not suggests that they represent distinct species. This same pattern of distribution is displayed by species of other genera from localities 2 and 3, e.g. among the hundreds of specimens of *Dimeropyge virginiensis* Whittington and Evitt (1954, pp. 37-42, Pl. 2, Pl. 3, figs. 1-30) are a small number that are distinctly different and do not grade morphologically into the common form, and which I regard as a separate species. One possible explanation of the "common" and "rare" species of the same genus at the same locality is that they represent sexually dimorphic forms of the same species, but this explanation can hardly be removed from the realm of speculation. In this connection Hintze (1953, p. 150) has discussed the occurrence of two pliomerid species at the same horizons of the Pogonip group, but in this case the two species are apparently equally abundant.

TABLE 4

Numbers of Exoskeletal Parts of all Sizes of *Apianurus* n.gen. and *Calipernurus* n.gen.

Locality	*Apianurus barbatus* n.gen., n.sp.			*Calipernurus insolitus* n.gen., n.sp.			*A. glaber* n.sp.			*A.* sp. ind.	
	Cranidia	Pygidia	Hypostomes	Cranidia	Pygidia	Hypostomes	Cranidia	Pygidia	Hypostomes	Pygidia	Hypostomes
2	115	82	15	21	17	2	13	20	5	12	4
3	95	58	17	12	6	0	0	9	0		
6	5	2	0								
8	28	56	28								

Apianurus glaber Whittington, n.sp.

Plate 21, figures 1-15.

Holotype: USNM 124703 (Pl. 21, figs. 1-3), locality 2.

Other Material: Paratypes, USNM 124704a, b; other figured material in USNM.

Geological Horizon and Locality: lower Edinburg limestone, localities 2, 3.

Description: Cranidium (Pl. 21, figs. 1-7, 11, 12) differs from that of *Apianurus barbatus* n.gen., n.sp. (Pl. 17, figs. 1-12) in that:

(1) Occipital ring with slightly depressed posterior band, widest (exs.) laterally, extremely narrow medially. In front of it a low ridge connects inner, posterior bases of occipital spines. Median occipital spine prominent, area between it and bases of occipital spines flattened, not evenly inflated. Paired occipital spines more divergent proximally, but curved so that distally they are directed slightly inward, not outward. Extremity of occipital furrow deeper, forming a more prominent projection on inner surface.

(2) Palpebral lobe less steeply inclined, eye ridge running forward and inward slightly farther out from lateral glabellar lobes, then curving more strongly in to meet frontal lobe of glabella. Anterior part of eye ridge less convex, and shallower depression outside it. Posterior border juts out slightly farther, and outer, sutural edge more acutely rounded.

(3) Larger cranidia with low tubercles on external surface, not curved spines. Tubercles are fewer in number than spines of *A. barbatus*, and on the glabella do not show any obvious paired arrangement. Lateral and postero-medial parts of occipital ring smooth. Smallest cranidia bear short spines on the glabella, few on occipital ring, but the fixed cheek bears spines with the characteristic *A. barbatus* curve, symmetrically arranged. These latter are reduced to rounded tubercles in the large cranidia, but retain the symmetrical arrangement.

A hypostome (Pl. 21, figs. 13, 14) from locality 2 differs slightly from that of *Apianurus barbatus* (Pl. 18, figs. 1-5), and is assigned to *A. glaber* principally because it is almost without ornament, there being only a few tubercles on the lateral border

adjacent to the shoulder. The outline is more rectangular, the median part of posterior margin being straight, the postero-lateral border broader. Middle furrow of middle body is distinct to midline, and does not fade out there, as in *A. barbatus*, and the same is true of the posterior border furrow.

Free cheek and thorax unknown. Pygidium attributed to this species (Pl. 21, figs. 8-10, 15) of the same form as that of *A. barbatus* (Pl. 18, figs. 11-13), with the same number of border spines but directed slightly more upward. Distinctive are the upright spines on pleural regions, short and inwardly curved, rather than long and curving back. Low tubercles on external surface, not short spines, a few on axial rings and scattered over pleural regions. Border and upright spines with lateral barbs. The reduction of the ornament on the axis reveals clearly the supposed areas of muscle attachment, over which the quartz is thinner. Three segments are distinct, the ring of the third outlined by an inverted V-shaped line of tubercles which enclose the tip of the axis. There is a median tubercle at the extreme tip, and between this and the ring of the third segment the quartz is also thin. This triangular area presumably represents the muscle attachments of a 4th segment.

Apianurus Whittington sp.ind.

Plate 21, figures 16-22, 25, 26.

Material: Figured specimens USNM 124705a-e, lower Edinburg limestone, locality 2.

Description: Pygidium known only from locality 2 and differs from that of *Apianurus barbatus* n.gen., n.sp. (Pl. 18, figs. 11-13) in that the pleural regions are relatively wider, the upright spine small and short, and there are one short and six long pairs of border spines, longer and slimmer and slightly more upwardly directed. The ornament is of typical curved spines like those of *A. barbatus*, and there are lateral barbs on upright and border spines. The smallest specimen (Pl. 21, fig. 21) is 1.6 mm. in width at the anterior margin, and exhibits the same distinguishing characters, except that there are 1 short and 5 longer pairs of border spines. However, pygidia of *A. barbatus* of this size also have one less pair of border spines.

A few specimens of a hypostome (Pl. 21, figs. 20, 22, 25, 26), occurring at locality 2, differ from that of *Apianurus barbatus* (Pl. 18, figs. 1-5) in the following respects: (1) smooth even curve of outline of anterior margin without the projection in front of middle body; (2) smooth curve, rather than V-shape, made by confluent middle furrows; (3) posterior lobe of middle body evenly inflated, not divided by a flattening near the midline; (4) lateral notch less well defined, anterior edge merging with adjacent border.

Both these exoskeletal parts are distinct from corresponding parts of *Apianurus barbatus* and *A. glaber,* and seem to represent at least one additional species.

Apianurus aff. furcata (Linnarsson, 1869)

Plate 20, figures 18, 20-25.

Material: PMO 66691a, incomplete cranidium; 66691b, small fragmentary cranidium; 66690, cranidium with incomplete occipital spines, all from Chasmops limestone, Guttormsberget; 3673, cranidium from Upper Chasmops limestone, Ferneholmen, Asker; 5647, pygidium from Bygdøy, near Oslo, Norway.

Geological Horizon: Chasmops limestone, middle Caradoc (Størmer, 1953, p. 130), or approximately late Black River or early Trenton (Twenhofel et al., 1954). The block from Bygdøy contains, besides the pygidium, cranidia and pygidia of *"Bronteopsis" gregaria* type (Cooper, 1953, Pl. 9) and *Remopleurides,* genera characteristic of the lower Edinburg of Virginia.

Description: Cranidium typical of the genus, differing from that of *Apianurus barbatus* n.gen., n.sp. (Pl. 17, figs. 2-12) principally in that: (1) occipital ring relatively a little longer and occipital spines more divergent; (2) fronto-median and fused lateral glabellar lobes less inflated; (3) palpebral lobe larger and less steeply sloping, and eye ridge just in front of lobe appears broader and more prominent. The tubercles of *A.* aff. *furcata* may be the bases of spines like those of *A. barbatus* n.gen., n.sp., and the number and distribution is similar.

The small pygidium (Pl. 20, fig. 20) is characteristic, having the large upright spine on the pleural region (broken off at the

base), and 6 pairs of border spines, the anterior pair small.

Discussion: The following species have been described from Sweden and the East Baltic:

Apianurus furcata (Linnarsson, 1869, p. 65, Pl. 1, fig. 18) cranidium from the Chasmops (=Beyrichia) limestone of Vastergötland, Sweden.

Apianurus kuckersiana (Schmidt, 1885, pp. 4-5, Pl. 1, figs. 2, 3; Öpik, 1937, p. 47, Pl. 24, figs. 3, 4) from the Kukruse (C_2) stage of Estonia. Öpik figured the characteristic pygidium as well as the cranidium.

Apianurus kuckersiana var. *mickwitzi* (Schmidt, 1907, pp. 23-24, Pl. 1, fig. 19), cranidium from the Keila (D_2) stage of Estonia.

Apianurus asklundi (Thorslund, 1940, pp. 154-155, Pl. 6, fig. 14), cranidium from the lower Chasmops limestone, Jemtland, Sweden.

All are from the Chasmops limestone or its equivalents, and presumably closely related. I have not had an opportunity to examine the original material, and so cannot venture an opinion as to how many species are represented. I have used the oldest specific name for the Norwegian material, rather than create another name. It is notable that many of the genera of trilobites of the lower Chasmops limestone listed by Thorslund (1940, pp. 184-185) occur also in the Edinburg limestone — e.g. *Trinodus*, *Remopleurides*, "*Bronteopsis*" (=*Stygina*? of Thorslund, 1940, p. 137), illaenids, *Dimeropyge*, *Ampyx*, *Lonchodomas*, *Sphaerexochus* (see Cooper, 1953; Whittington and Evitt, 1954).

Apianurus clevei (Warburg, 1925, pp. 243-245, Pl. 6, fig. 1), a cranidium from the Upper Ordovician Boda limestone of the Siljan district, central Sweden, appears to represent the youngest known species of *Apianurus*. Warburg also described a hypostome (1925, pp. 253-254, Pl. 6, fig. 7) and an incomplete pygidium (pp. 241-242, Pl. 6, fig. 9) from other localities in the Boda limestone which may well represent this same species.

Genus CALIPERNURUS Whittington, n.gen.

Type Species: *Calipernurus insolitus* Whittington n.gen., n.sp.

Diagnosis: Differs from *Apianurus* in that: (1) Cephalon is

relatively wider, six-sided rather than ovate in outline, and less deep; (2) occipital ring with lateral regions more sharply set off from swollen median portion, occipital spines diverge at 90° or more and directed close above thorax; (3) eye lobe farther for-

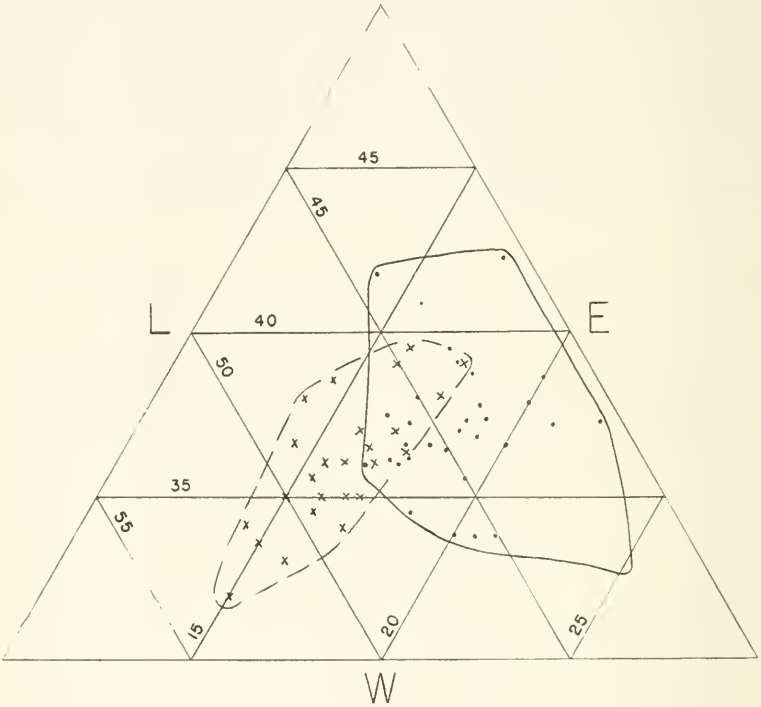


Figure 23. Triangular graph comparing relative dimensions of cranidia of *Apianurus barbatus* n.gen. n.sp. (shown by dots enclosed by solid line, the dot in the lower right-hand corner has been accidentally omitted — compare Text-fig. 21.) and *Calipernurus insolitus* n.gen., n.sp. (shown by crosses enclosed by broken line). L, sagittal length of cranidium. W, width between spines B on posterior border. E, length (exs.) from anterior margin to midpoint of palpebral lobe. Measurements were made in exterior view, i.e. with isolated cranidium resting on a horizontal surface.

ward, opposite first glabellar furrows; (4) pygidium with 4 lateral and one median border spine, posterior three of equal size, major spines on pleural regions directed backward and

slightly upward, curving inward in caliper-shape; (5) ornament of large tubercles rather than slim, thorn-like spines or small tubercles.

Geological Range: Middle Ordovician.

Discussion: Text-figure 23 illustrates the generally greater width of cranidia of *Calipernurus* compared to those of *Apianurus*, and the greater distance from the anterior margin back to the palpebral lobe in *Apianurus*.

At least four species of *Apianurus* are here recognized, from the Appalachian, Scandinavian and Baltic areas. All have the less divergent occipital spines, and the associated pygidium has pairs of border spines and the upright major spines. The *Calipernurus* type of cranidium and pygidium seems to be known only from Virginia, and is here regarded as representing a different but evidently closely allied group, of generic rank.

Calipernurus insolitus Whittington, n.gen., n.sp.

Plates 22-24; Text-figures 23, 24.

Holotype: USNM 124711 (Pl. 22, figs. 1-3, 6; Pl. 23, figs. 1, 3). Locality 3.

Other Material: Paratypes, USNM 124712 a-d; all figured material in USNM.

Geological Horizon and Localities: Lower Edinburg limestone, localities 2, 3.

Description: Cephalon wider than long, outline (ignoring major spines) roughly six-sided; cranidium trapezoidal in outline, anterior margin less than half width of posterior. Glabella widest at occipital ring, occipital furrow shallow medially, outer part deep, diagonally directed outward and forward. Median part of occipital ring considerably higher than lateral, and bearing a short, stout median tubercle and the occipital spines; latter diverge at 90° or more (more in most larger specimens), proximal part straight and directed low over thorax, distal part curved inward and tapering. Fronto-median glabellar lobe subparallel-sided, gently convex posteriorly, moderately convex anteriorly, sloping steeply down to shallow preglabellar furrow. Portion between basal lateral lobes merges with these lobes, and is set off by faint transverse depression almost in line with pits representing basal glabellar furrows; greatest convexity of

fronto-median lobe in front of this depression. First and second glabellar lobes fused, kidney-shaped in outline and gently convex, separated by change in slope from fixed cheeks, posterior lobe slopes vertically to occipital furrow, second separated by sharp change in slope from median. First and second glabellar

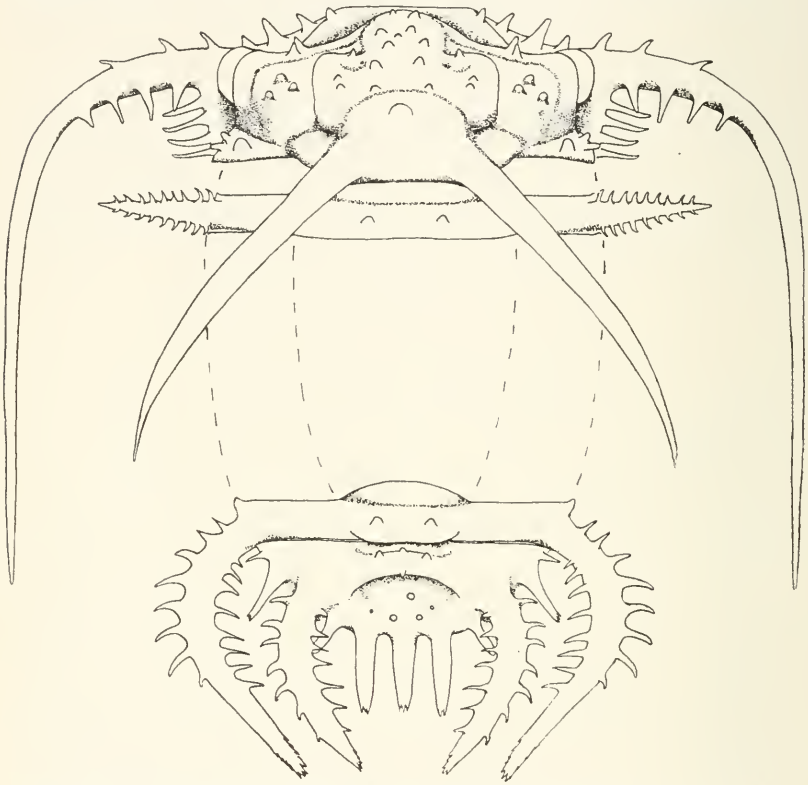


Figure 24. *Calipernurus insolitus* n.gen., n.sp. Reconstruction, dorsal view, number of thoracic segments unknown. Approximately X 10.

furrows represented by circular depressions, the first at the inner margin of the fused lateral lobes, the second at the inner, anterior corner of these lobes. Highest point of large eye lobe on transverse line passing just behind first glabellar furrows and level with crest of glabella in this line. Palpebral lobe slopes

steeply, broad rim passes into broad, convex eye ridge which runs straight inward at 45°, passes close to antero-lateral margin of fused lateral lobes and merges into frontal glabellar lobe. Eye surface hemispherical (Pl. 23, figs. 9, 10), outer surface almost smooth, facets faintly visible on inner surface. Anterior branch of suture runs on low sutural ridge straight forward and inward to anterior margin, where it meets rostral and connective suture. Posterior branch of suture runs back in line with anterior branch across border, then curves inward across doublure. Anterior border narrow (sag.) medially, becoming wider laterally and merging with sutural ridges. Deep depression parallels eye ridge on outer side, separating it from border and sutural ridge. Fixed cheek inside eye lobe slopes gently inward to margin of fused lateral glabellar lobes, inside and behind eye lobe it slopes steeply, almost vertically, down to occipital ring and posterior border furrow. Latter commences at lateral margin of occipital ring and runs forward and outward, so that convex border is widest at suture. Free cheek narrow, librigenal spine arises in front of eye lobe and curves outward and backward, the distal part directed straight back. Lateral border gently convex, defined by shallow border furrow, and runs from posterior branch suture to merge with swollen base of librigenal spine. No antero-lateral border is defined, though there is a depression between the sutural ridge and swollen base of the librigenal spine. Shallow antennal notch in vertical border of free cheek adjacent to anterior suture (Pl. 23, fig. 1). Doublure of free cheek widest behind notch, narrowing back and ending at posterior suture. Posterior border without doublure, articulating socket just inside suture. On inner surface of cranidium (Pl. 23, fig. 4) doublure of occipital ring and ridges, made by outer parts occipital furrow, are seen. First, and especially second glabellar furrows, and depression outside eye ridge, also project ventrally. Rostrum unknown, but evidently (Pl. 23, fig. 1) broad (tr.) and short (sag. and exs.), lateral margins converging backward, fitting so that outer surface faces almost directly downward. Two specimens only are known of the hypostome (Pl. 23, figs. 11-15). Anterior margin projects forward in front of convex middle body. Latter divided by shallow middle furrows which run inward and backward to about three-quarters

of the length and do not reach the midline. Posterior lobe crescentic, convex, especially toward the tips. Lateral borders horizontal, shallow border furrows, shallow lateral notch and sharply-pointed shoulder. Posterior border little wider than lateral, bent to slope steeply dorsally, border furrow shallow. Doublure widest at shoulder, where it is crossed by a sharp ridge, narrowest posteriorly. Tiny perforation just behind shoulder ridge (Pl. 23, fig. 15). The smaller specimen (Pl. 23, figs. 13, 14) has short, triangular anterior wings, but these are absent in the larger specimen (Pl. 23, figs. 11, 12, 15) and both antero-lateral corners are cut off. This truncation seems not to be accidental breakage, but is symmetrical. This hypostome differs from that of *Apianurus* (Pl. 18, figs. 1-5) in the much greater inflation of the middle body posteriorly, less distinct middle furrows, inclination of posterior border, smaller lateral notch, smaller opening in doublure, and ornament. It is accordingly regarded as probably belonging to *Calipernurus*.

External surface of cephalon with scattered tubercles, area between them, and all furrows, smooth. Largest is the median occipital tubercle, in the rounded top of which are four tiny depressions set at the corners of a square (Pl. 23, figs. 7, 8). Next largest in size are various symmetrically placed tubercles — pairs on the fronto-median and lateral glabellar lobes, pair at antero-lateral corners of cranidium, pair on outer edge of eye-ridge at midlength, three just inside eye on fixed cheek, and one about at midpoint, one at extremity, of posterior border. Smaller tubercles are scattered, some symmetrically, on the cranidium and free cheeks, including base of librigenal spines. On the borders of the free cheek and proximal part of the librigenal spine are thorn-like spines, constant in number, position and direction. On the librigenal and occipital spines are short spines directed distally at a low angle to the axis of the spine, and becoming longer distally. There are openings at the base of these spines on the distal side (Pl. 23, fig. 6), but tubercles and spines elsewhere on the cranidium seem to be imperforate, and the bases of the tiny depressions in the occipital tubercle seem to be closed. Hypostome with tubercles on lateral borders only.

Few thoracic segments known, and number in thorax unknown; reconstruction (Text-fig. 24) assumes number was 10.

One segment from anterior part of thorax (Pl. 24, figs. 15, 16, 19) shows relatively wide, convex axis and horizontal, unfurrowed pleurae. Extremity of articulating furrow deep, articulating half ring as long (sag.) as axial. Pleural spines curving out and down, directed slightly forward. Doublure rolled under at base spine, and articulating process on anterior edge, socket on posterior edge. Smooth band runs across highest part of axial ring and pleurae into base pleural spine. Tubercles outside this band, some larger ones on posterior edge axial ring and on slope of articulating furrow paired. Lateral margins of pleural spine with row of close-spaced, curved spines. Two incomplete segments from the posterior part of the thorax, and an incomplete segment, possibly the posterior (Pl. 24, figs. 22, 23, 26), have the pleural spine curved like that of the major pygidial pleural spine. Smooth median band, and larger tubercles on posterior edge of axial ring and flanges of pleura are rounded like those of the cephalon, some on the axis paired. These segments are placed in *Calipernurus* because smooth band resembles that on occipital ring and posterior border (Pl. 23, fig. 5), deep extremities of articulating furrow resemble those of occipital furrow, and because pleural spines and bands on them are like those of major pleural spine of the pygidium.

Pygidium (Pl. 24, figs. 25, 27, 28) more than twice as wide as long, axis of same width as pleural region at anterior margin. First axial ring prominent, in front of it shallow articulating furrow and long (sag.) articulating half-ring. Posterior edge of axial ring descends vertically to gently convex posterior part of axis, which merges into pleural regions except antero-laterally, where shallow depressions occur. First axial ring connected across pleural lobes by low pleural ridge to base of major pleural spine, which arises inside margin and curves upward and inward. Rest of pleural regions flat, margin rolled, no border furrow. From vertical margin of border, four pairs and one median posterior spine arise — a pair of similar size flanking the median spine, a short pair just inside and beneath the major spine, and two pairs in front, the anterior tiny. Two specimens (Pl. 24, figs. 11, 18) lack the median border spine, and one (Pl. 24, fig. 17) has the median bifurcate at the tip, but lacks the pair flanking it. Such variation is unusual in this material.

Doublure sharply bent up, widest posteriorly, appendifers not developed, but areas of muscle attachment (shown by thinness of quartz) include extremities of articulating furrow, and corresponding areas behind first ring. In some species the entire area of the axis behind the ring is of thinner quartz, suggesting that it is all an area of muscle attachment. Ornament of rounded tubercles, paired and median on axial ring, pair at center of rest of axis, row of two or three at tip. Other tubercles on anterior region of pleural regions and base of major pleural spines. Latter with row of curved, thorn-like spines along lateral margins, also tubercles and distally-directed sharp tubercles, near tip. Latter have openings at base on distal side (Pl. 24, figs. 21, 24). Other border spines with short spines scattered on them, not in regular rows, directed distally at tips and with openings.

Development. Cranidium. Smallest known cranidium (Pl. 24, fig. 1) of length (sag.) 0.78 mm. Occipital spines diverging at about 90°. Glabella convex, parallel-sided, occipital ring prominent, with median tubercle and paired spines; fronto-median lobe with 5 pairs of axial spines — 2a, 2, 3, 4, and 5. Extra spine on left side between 3 and 4, median spine between 4 and 5. Median lobe between spines 2a and 2 with slight extra inflation. Basal glabellar lobe small, gently inflated ovate area low on side of fronto-median lobe, one median spine; second glabellar lobe smaller and fainter. Palpebral lobe situated in front of half length of cranidium, strongly raised, low eye ridge runs forward and inward. Narrow anterior border; posterior border widens (exs.) outward. Most prominent spines on fixed cheek include A_1, A_2, A_3, B, C, Pl, Er, and one of similar size at extremity of anterior border. Larger cranidium 1.08 mm. in length (sag.) (Pl. 24, figs. 5-7) has similar glabella, but the lateral lobes are larger, more inflated, separated by the subcircular pit of the first lateral furrow. Palpebral lobe larger, higher, slightly farther back, eye ridge more prominent, and steeper slope of cheek behind palpebral lobe. Free cheek is like larger ones, except eye surface is farther forward.

With further increase in size (Pl. 24, figs. 2-4, 9) the main changes are widening and elevation of the lateral glabellar lobes so that they become fused outside the first lateral furrow, the

axial furrows stand higher, and thus the fixed cheeks slope less steeply inward. The eye lobe moves back, and the slope behind it becomes steep. Additional spines appear, and the larger ones are reduced to high tubercles. In cranidia of length (sag.) 1 to 2 mm. some 40 per cent of the specimens have the occipital spines diverging at less than 90°, whereas the remainder and all larger specimens have them diverging at 90° or more.

The close similarity between the development of the cranidium of *Calipernurus* and that of *Apianurus* is evident.

Pygidium: A transitory pygidium (Pl. 24, fig. 12) of Stage holaspis-1 has the first segment marked off by interpleural grooves, and the long pleural spines curve inward and backward. The pleural spines of the second segment are only slightly curved, and more inwardly directed. The posterior border bears three border spines. Axis of 3 rings, anterior with 2 pairs and a median spine, second two with one pair each. This specimen shows that the major pleural spines of the true pygidium correspond to the pleural spines of the thorax. Smaller transitory pygidia have not been recognized, but they would evidently be extremely similar to some of those here regarded as representing *Apianurus barbatus,* n.gen., n.sp. (Pl. 19, figs. 24, 25, 27-29). Small true pygidia (Pl. 24, figs. 8, 13, 14) have the additional pairs of border spines, though the anterior is extremely small.

Subfamily SELENOPELTINAE Corda, 1847

(=Selenopeltides Corda, 1847, p. 33, and Selenopeltidae Prantl and Přibyl, 1949, p. 172)

Genus SELENOPELTIS Corda, 1847

Text-figure 25.

Synonym: *Polyeres* Rouault, 1847, type species by monotypy *P. dufrenoyi* Rouault, 1847; see Clarke, 1892, p. 96; Prantl and Přibyl, 1949, pp. 173-175.

Diagnosis: Cephalon transversely subrectangular in outline. Glabella gently convex, tapering slightly forward, occipital ring short (sag. and exs.), low median tubercle; wide fronto-median lobe, convex band across base; apparently three lateral glabellar lobes, defined by faint axial furrow, shallow first lateral and

deeper second lateral furrow, and by longitudinal furrow joining first lateral to occipital furrow, anterior part of this longitudinal furrow deep; basal lobe divided subequally by faint transverse furrow and posterior portion subdivided by longitudinal furrow. Inner corner of cheek inflated, merging into antero-lateral part of occipital ring. Crescentic eye lobe at about half length (exs.) of cheek and in inner part. Librigenal spine stout, long, directed upward and outward, no spines on anterior and lateral borders of cheek. Hypostome subrectangular in outline, wider than long, shallow median posterior notch, wide postero-lateral border; middle furrow broad, shallow, running in from antero-lateral corner of middle body. Thorax of 9 segments, axial rings with prominent lateral lobes, horizontal pleurae with ridge running in curve convex forward which distally runs out into long posterior pleural spine; anterior pleural spine downwardly and outwardly directed, curved. Pygidium with short axis and one pair border spines only, connected to first ring by prominent pleural ridge. External surface tuberculate or granulate.

Geological Range: Lower to Upper Ordovician.

Discussion: The peculiarities of this genus have long been recognized, and include the shortness of the occipital ring, the partial fusion of the basal and median glabellar lobes and subdivision of the former, the conspicuous lateral lobes of the thoracic axial rings, the forward curve of the main ridge of the pleura, and the lack of spines along the borders of the free cheek and pygidium (excepting the major pair). The anterior pleural spine was figured by Barrande (1852, Pl. 36. fig. 6; Pl. 37, fig. 25), and is curved, projecting downward and outward below the posterior pleural spine of the preceding segment.

Selenopeltis is here regarded as belonging within a separate subfamily (rather than family). I agree with Prantl and Přibyl, (1949, p. 173) than *Selenopeltis* has affinities with the Mira-

Figure 25. *Selenopeltis buchi* (Barrande), Middle Ordovician, Bohemia. Approximately X ⅘. A, cephalon, anterior view, based on MCZ 4317, Chlustina Beds, de_{2b}, "Brdatka" near Beraun. B, hypostome, exterior view, based on MCZ 4316, Drabov quartzites, dδ, Drabov. C, exoskeleton in dorsal view, based on MCZ 4319, Sárka Shales, $d\gamma_1$, Osek, MCZ 4316, MCZ 4317, etc.

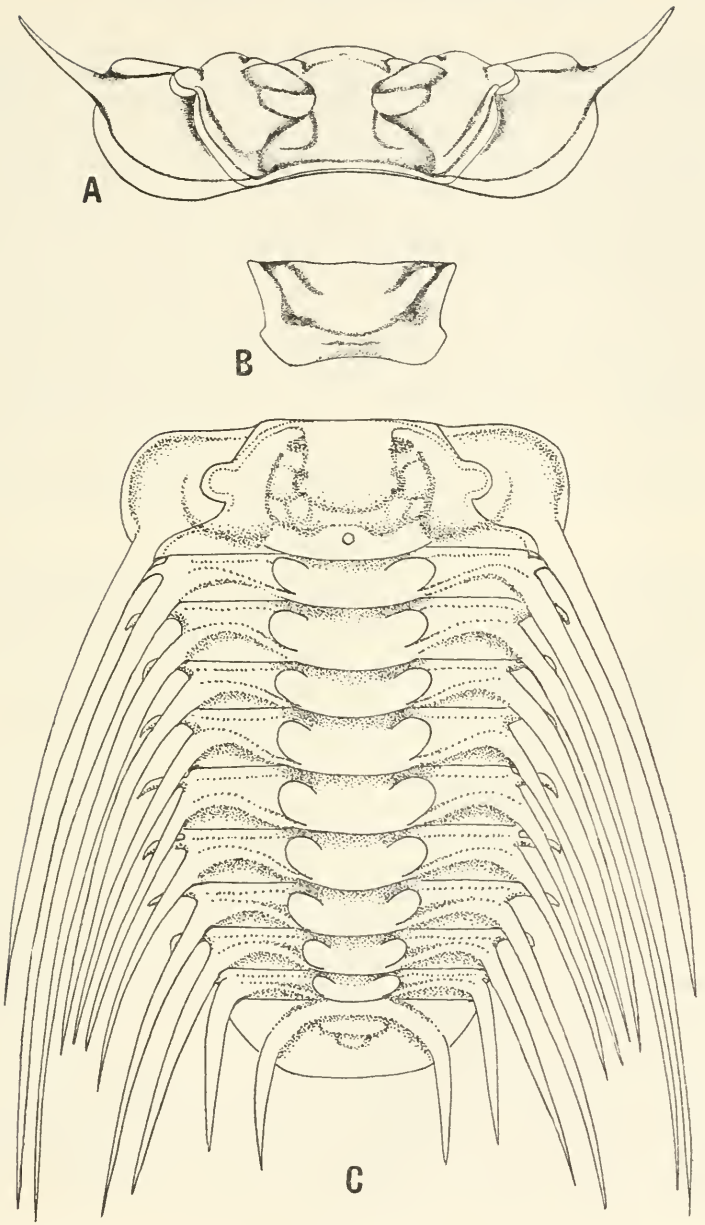


Figure 25

spinae rather than with other subfamilies, particularly in the general form of the cephalon, and notably the hypostome. But *Selenopeltis* shares many odontopleurid characters with other genera, and some of its peculiar features appear in these other genera. For example, *Dicranurus* also lacks spines on the lateral cephalic border; the curve of the pleural ridge in *Selenopeltis* is an accentuation of the same curve seen in such genera as *Miraspis* and *Dicranurus;* fusion of median and basal glabellar lobes occurs in *Apianurus*, n.gen.

Selenopeltis is well known from the Llanvirn to Ashgill of Bohemia, has been recorded in France, and more recently in Morocco (Termier and Termier, 1950, Pl. 194, figs. 1-4), and Shropshire (Whittard, 1952, p. 158), the latter in rocks of Arenig age.

Other Genera, Subgenera and Species Sometimes Referred to Odontopleuridae

Acidaspis ulrichi Bassler, 1919 (pp. 355-356, Pl. 37, figs. 6-8) is part of an Upper Cambrian trilobite (Wilson, 1952, p. 317), presumably the free cheek, and of unknown affinities.

Acidiphorus Raymond, 1925. Not an odontopleurid, probably a bathyurid (Whittington, 1953, p. 669).

Ancyropyge Clarke, 1892. Based on a pygidium, recently redescribed (Stumm, 1953, p. 126, Pl. 6, figs. 1, 2), and may be an odontopleurid.

Bounyongia Etheridge and Mitchell, 1917, type species by monotypy *B. bowningensis* Etheridge and Mitchell, 1917. Based on two poorly preserved specimens of the cephalon, one with a few thoracic segments attached, recently said by Gill (1948, p. 18) to be a subgenus which "must now lapse," since the character upon which it was founded — a pair of cephalic spines arising from the glabella — is a misinterpretation, the spines being occipital. Prantl and Přibyl (1949, p. 181) regarded *Bounyongia* as a synonym of *Ceratocephala.*

Glaphurus Raymond, 1905, and *Glaphurina* Ulrich, 1930. In 1913 Raymond (p. 723) placed the former genus in the Odontopleuridae, but later (1916, p. 138) thought it should be excluded. Hupé (1953, p. 229) comments on the apparent odontopleurid

characters. I consider the resemblance superficial, and agree with Hupé that these two genera may be placed in a separate family, allied to Telephidae (Hupé, 1953, pp. 228-230).

Globulaspis Reed, 1931, type species *Acidaspis* (*Globulaspis*) *prominens* Reed, 1931 (pp. 100-101, Pl. 5, figs. 5, 5a, 5b), from the Lower Silurian of southern Scotland. The holotype, the internal mould of an incomplete cranidium, appears to be unique. I do not think it shows much resemblance to *Whittingtonia,* as do Prantl and Přibyl (1949, pp. 133-134), and am not sure that it is an odontopleurid.

Pharostoma Corda, 1847, and *Ptychometopus* Schmidt, 1894, have sometimes been excluded with question from the Calymenidae, and comments have been made regarding their odontopleurid-like appearance (cf. Shirley, 1936, pp. 385-386; Öpik, 1937, p. 24). I consider this resemblance probably superficial, and that these genera belong with the calymenids (cf. Hupé, 1953, p. 232).

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EXPLANATION OF PLATES 1-24.

To make the photographs, the larger specimens were mounted on insect pins with gum arabic, the smaller specimens laid on a black surface. A light coating of ammonium chloride was used. Stereoscopic pairs of views were made by tilting the specimen, and only the left-hand view of a pair is numbered. The heads and shafts of the pins have been blacked out; otherwise the photographs have not been retouched. It is arbitrarily decided that the plane passing through the margin of the occipital or axial ring shall run in the dorso-ventral direction, and views are described accordingly. Exterior or interior views have been taken in a direction lying in the sagittal plane to give the fullest possible view of the exoskeletal surface. Oblique exterior or interior views have been taken in directions at an angle to the sagittal plane. The initials USNM refer to the U. S. National Museum, Washington, D. C., and the initials PMO to the Museum of the Paleontological Institute, Oslo, Norway. These initials are followed by the catalogue numbers.

Plate 1

Primaspis ascitus n.sp.
Lower Martinsburg shale, locality 10

Figure

1, 2, 5. Holotype cranidium, paratype free cheek: dorsal and antero-lateral stereographs, anterior view, X 6. USNM 116515, 116516a.

3, 7, 9, 10. Paratype pygidium: posterior, left lateral views; dorsal, ventral stereographs, X 6. USNM 116516e.

4. Paratype free cheek: oblique interior view, X 9. USNM 116516a.

6. Holotype cranidium: interior stereograph, X 6. USNM 116515.

8, 11, 12, 13. Paratype segment: right lateral view; dorsal stereograph; anterior, posterior views, X 4. USNM 116516c.

14. Paratype thoracic segment: dorsal stereograph, X 4. USNM 116516d.

15, 17. Incomplete posterior thoracic segment; interior, exterior views, X 9.

16. Small pygidium: dorsal view, X 15.

18, 19, 20, 21. Paratype hypostome: posterior, anterior views; exterior, interior stereographs, X 6. USNM 116516b.

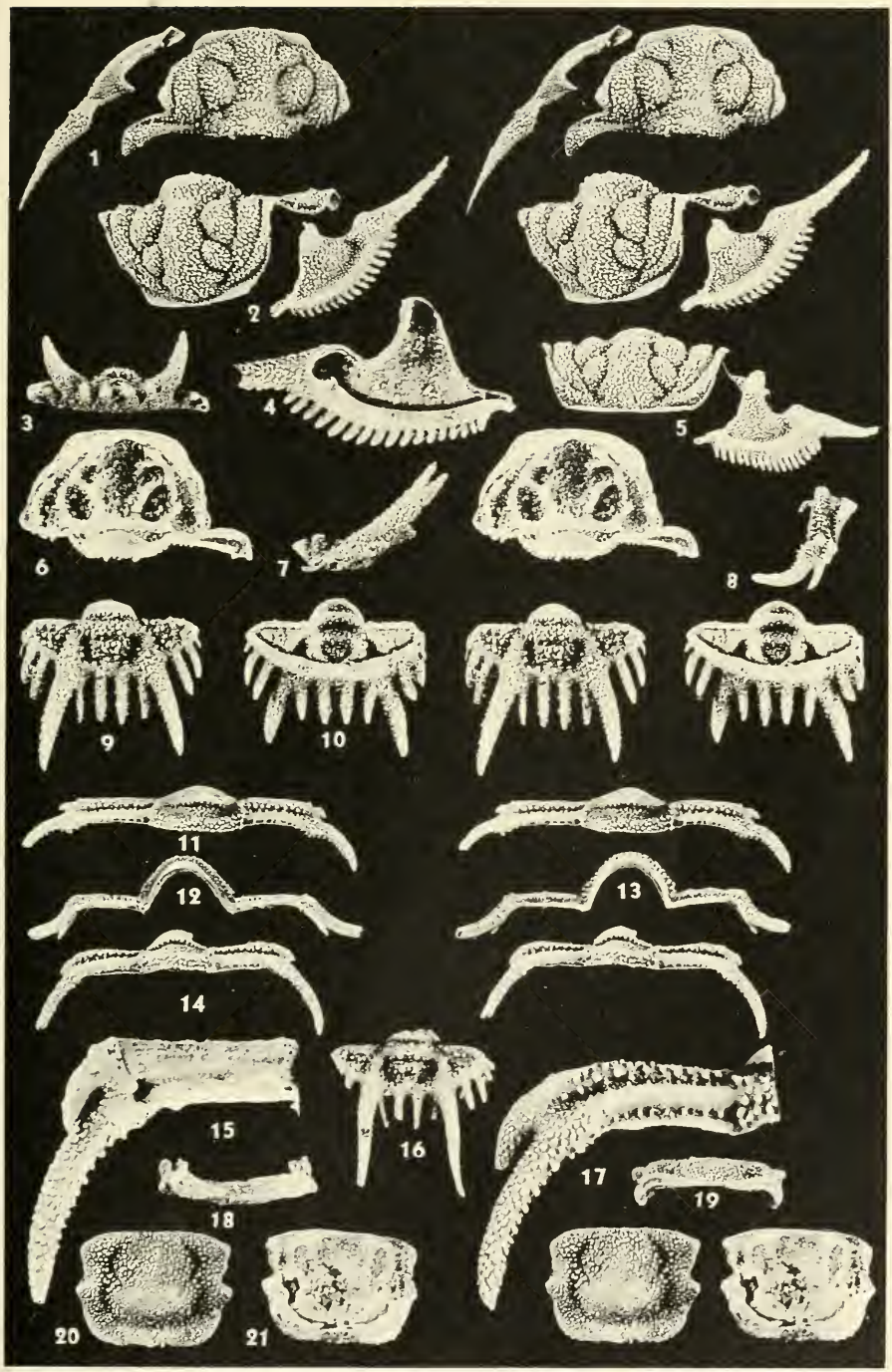
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PLATE 2

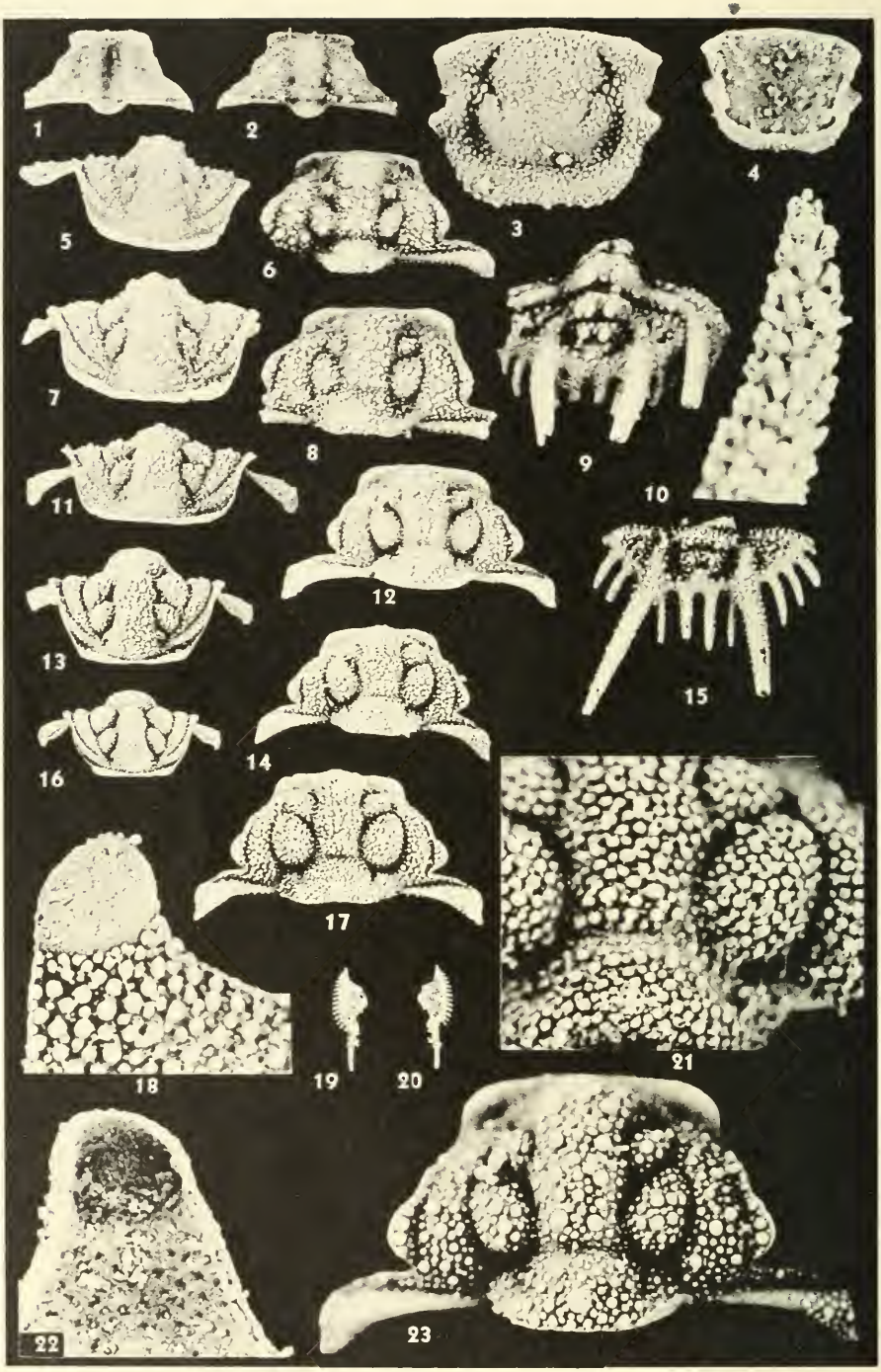

Plate 2

Primaspis ascitus n.sp.
Lower Martinsburg shale, locality 10

Figure

1, 2. Small cranidium: interior, exterior views, X 220. Original of Text-figure 6A.

3, 4. Small hypostome: exterior, interior views, respectively X 30, X 20.

5, 6. Small cranidium: anterior, exterior views, X 20. Original of Text-figure 6B.

7, 8. Small cranidium: anterior, exterior views, X 20.

9. Transitory pygidium: dorsal view, X 30.

10. Tip of posterior pleural spine showing openings between tubercles, X 30.

11-12, 23. Small cranidium: anterior view, X 15; dorsal views, respectively X 15, X 30.

13-14. Small cranidium: anterior, dorsal views, X 10.

15. Small pygidium: dorsal view, X 15.

16-17. Small cranidium: anterior, dorsal views, X 10.

18,22. Paratype free cheek: oblique exterior, oblique interior views of eye surface, X 30. USNM 116516a.

19,20. Small free cheek: oblique interior, oblique exterior views, X 20. Original of text-figure 6B.

21. Holotype cranidium: basal portion of glabella showing external surface, X 20.

Plate 3

Diacanthaspis cooperi Whittington
Lower Martinsburg shale

Figure

1, 2, 5, 6. Protaspis: exterior, interior stereographs; postero-dorsal, antero-dorsal views, X 50. Locality 12. Original of Text-figure 9A, B.

3-4. Stage 0 exoskeleton: exterior, interior, stereographs, X 50. Locality 12. Original of Text-figure 9C.

7, 9-10. Hypostome: exterior stereograph; interior, oblique interior views, X 10. Locality 10.

8. Small cranidium and free cheek: exterior stereograph, X 20. Locality 10. Original of Text-figure 9D.

11. Anterior thoracic segment: dorsal view, X 6. Locality 10.

12. Median thoracic segment: dorsal view, X 6. Locality 10.

13. Small hypostome: exterior view, X 30. Locality 10.

14. Small hypostome: oblique interior view showing hole in doublure, X 30. Locality 10.

15-16. Incomplete posterior thoracic segment: dorsal, left lateral views, X 6. Locality 10.

17-18. Stage 8 transitory pygidium: exterior, interior views, X 30. Locality 12.

19. Holaspid pygidium: dorsal stereograph, X 4½. Locality 12.

20. Tip of genal spine: oblique exterior view, X 30. Locality 9.

21. Eye surface: oblique exterior view, X 30. Locality 9.

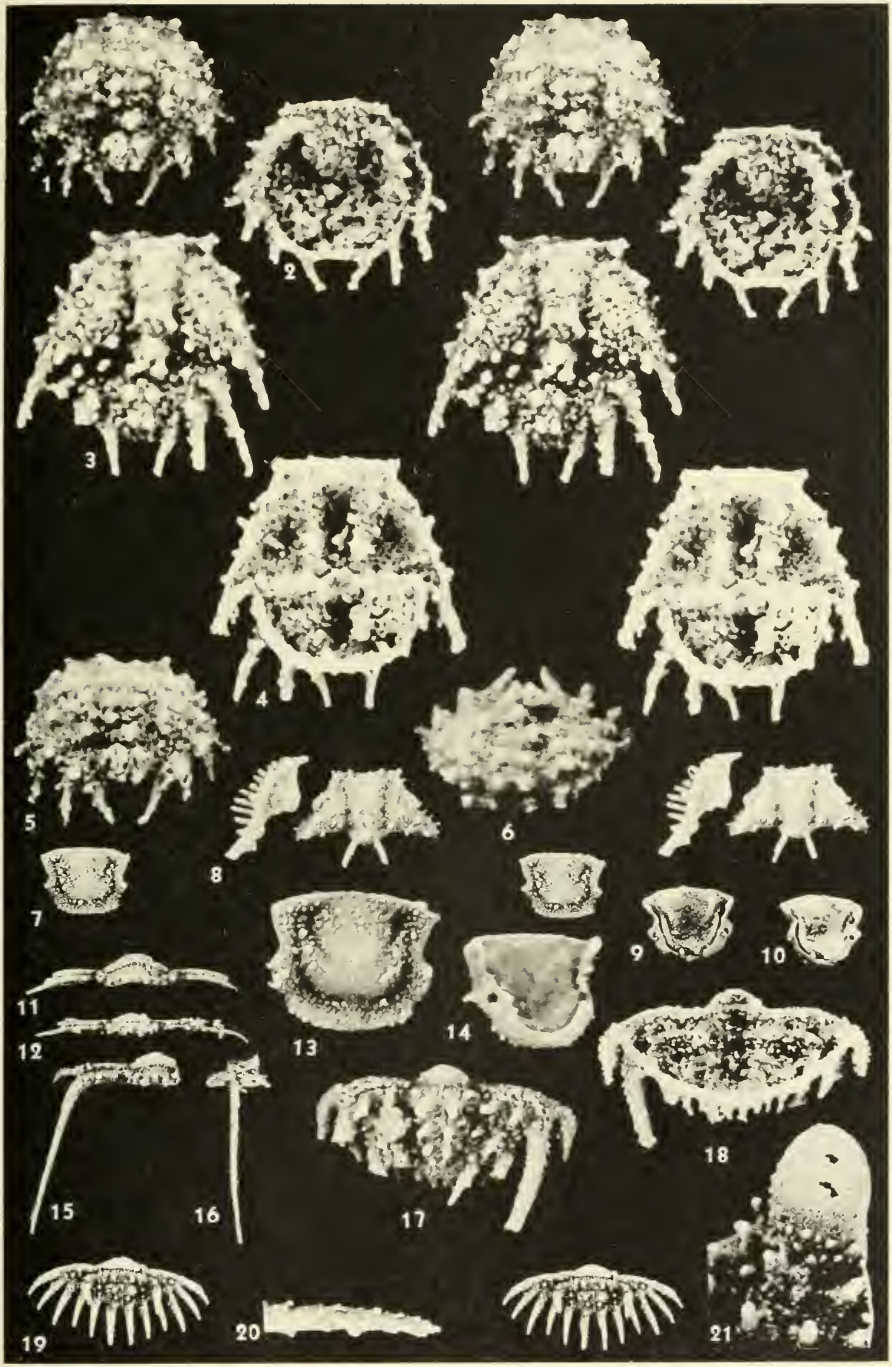
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PLATE 4

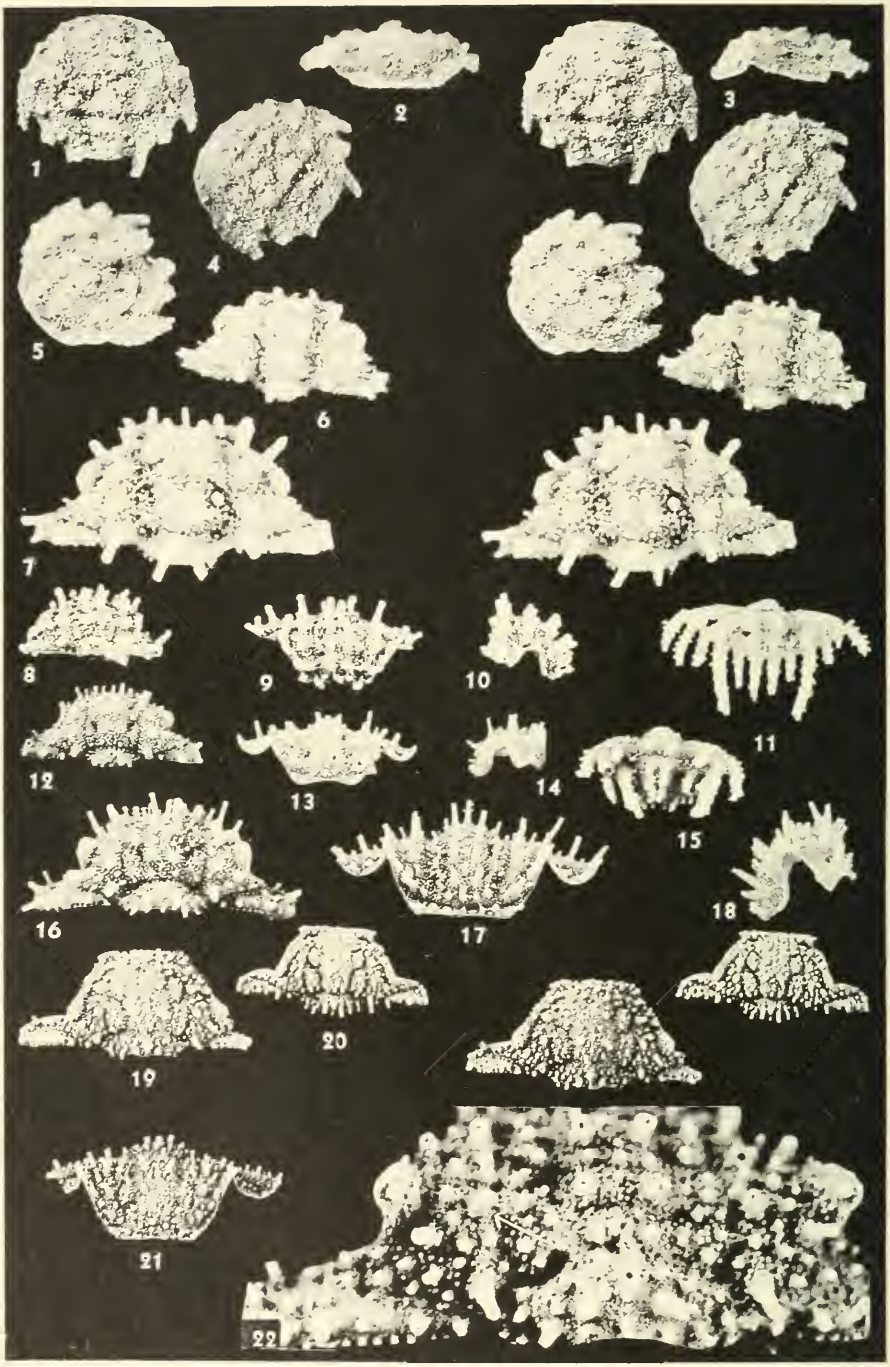

PLATE 4

Diacanthaspis lepidus n.sp.
Lower Edinburg limestone

Figure

1, 2, 3, 4, 5. Incomplete protaspis: exterior stereograph, anterior view, left lateral view, postero-dorsal stereograph, antero-dorsal stereograph, X 33.6 Photograph by W. R. Evitt. Locality 4.

6. Small cranidium: exterior stereograph, X 30. Locality 3.

7. Small cranidium: exterior stereograph, X 30. Locality 3.

8, 9, 10. Small cranidium: dorsal, anterior, right lateral views, X 15. Locality 3.

11. Small pygidium: dorsal view, X 20. Locality 2.

12, 13, 14. Small cranidium: dorsal, anterior, left lateral views, X 15. Locality 2.

15. Transitory pygidium: dorsal view, X 30. Locality 4.

16, 17, 18. Small cranidium: dorsal, anterior, left lateral views, X 15. Locality 2.

19, 21. Cranidium: exterior stereograph, anterior view, X 6. Locality 2.

20. Cranidium: exterior stereograph, X 6. Locality 2.

22. Posterior part of cranidium: exterior view, X 30. Locality 2. Arrow points to spine with truncated tip and tiny depressions or openings.

Plate 5

Diacanthaspis lepidus n.sp.
Lower Edinburg limestone

Figure

1, 7, 9. Holotype cranidium and paratype free cheek: dorsal stereograph; anterior, oblique exterior views, X 10. USNM 116517, 116518a. Locality 2.

2, 3, 5, 6. Incomplete thoracic segment: exterior, anterior, posterior, interior views, X 12.5. Locality 4.

4. Holotype cranidium: interior view, X 15. USNM 116517. Locality 2.

8, 13, 14. Pygidium: interior view, X 6; posterior and right lateral views, X 4. Locality 2.

10, 11. Part of thorax and pygidium, paratype: dorsal and ventral stereographs, X 6. USNM 116518c. Locality 3.

12. Pygidium: dorsal stereograph, X 9. Locality 2.

15, 16, 17, 18. Paratype hypostome: interior stereograph, X 20; exterior stereograph posterior and anterior views, X 15. USNM 116518b. Locality 3.

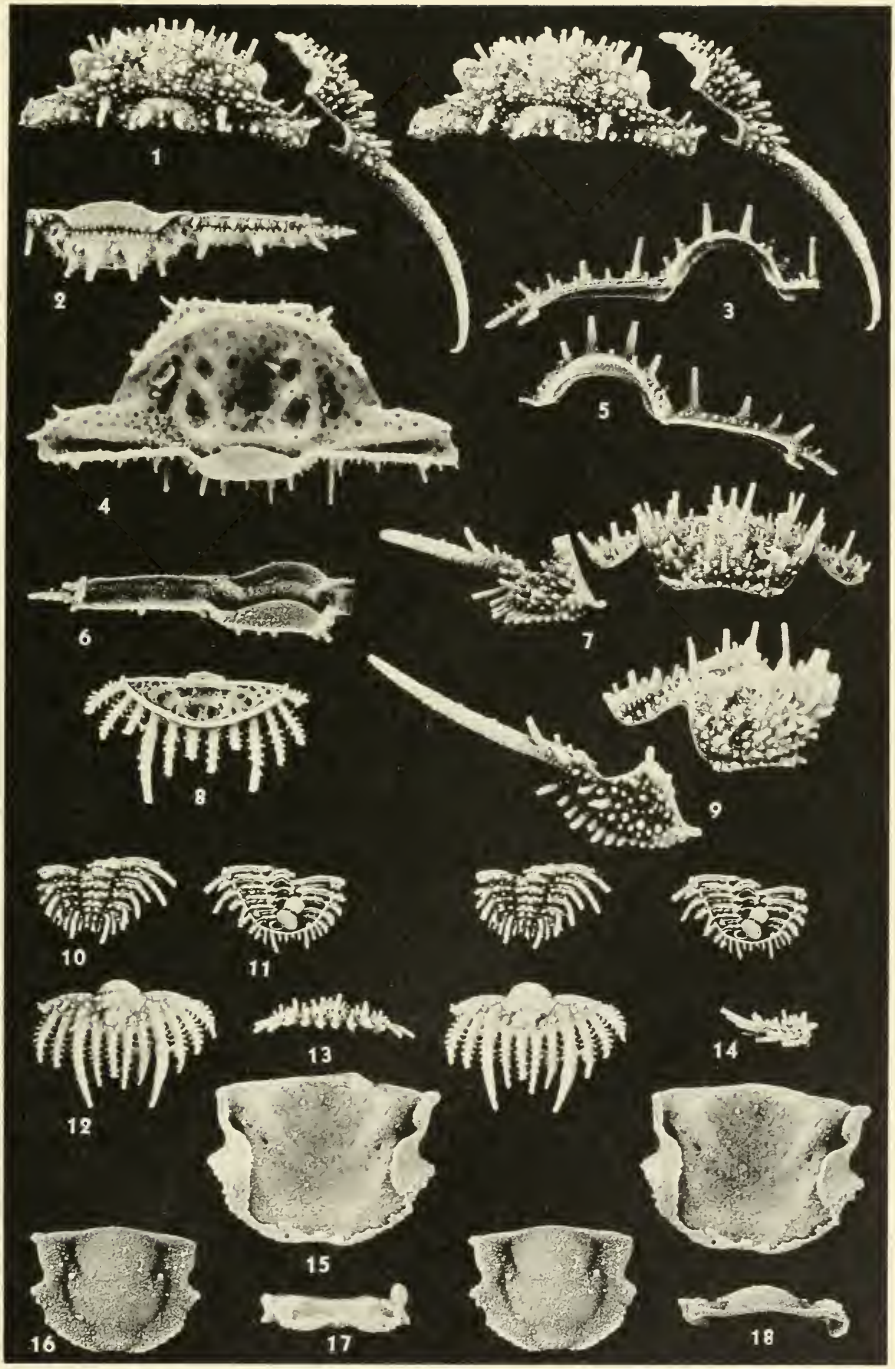
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PLATE 6

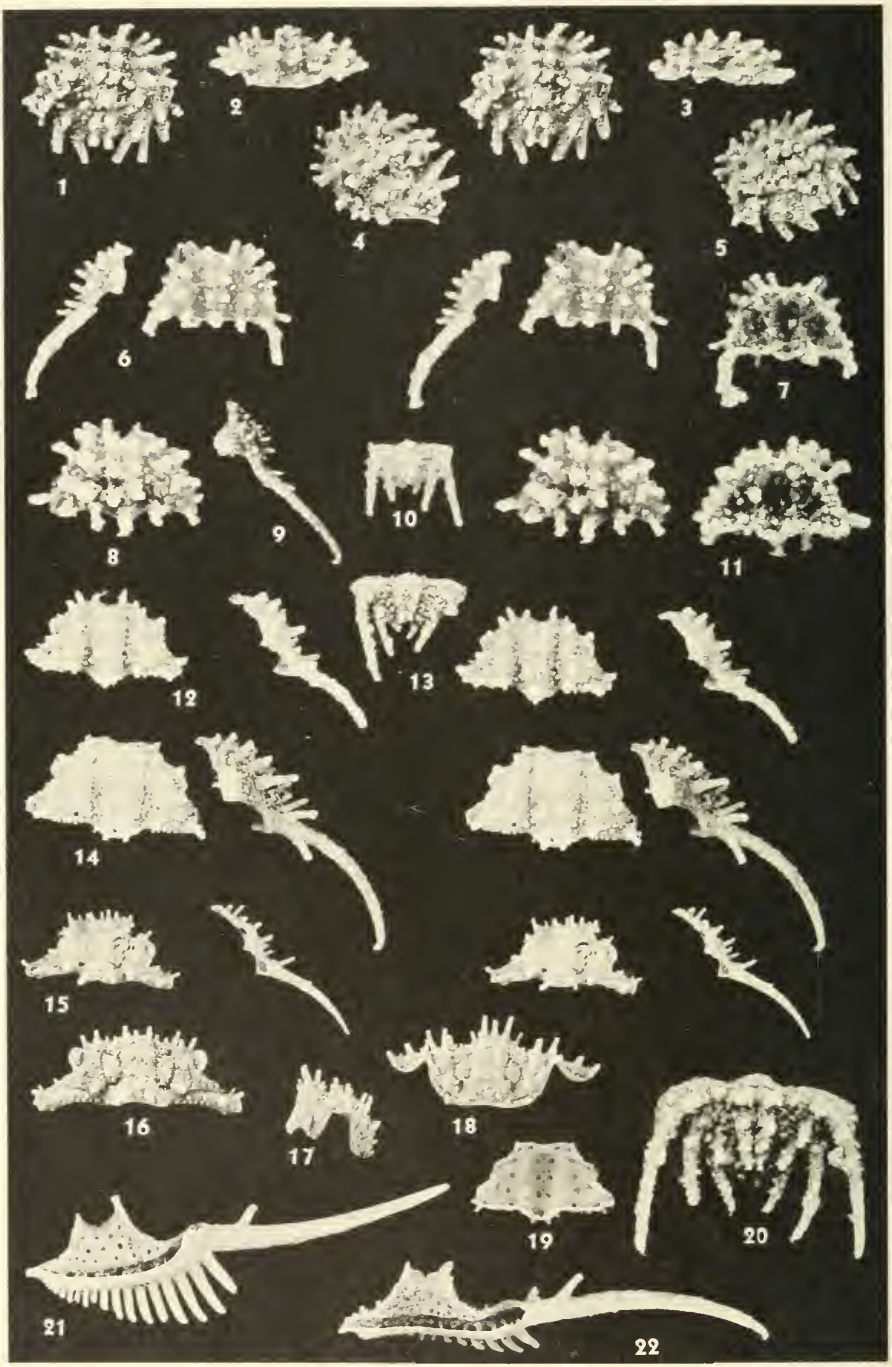

Plate 6

Diacanthaspis secretus n.sp.
Lower Edinburg limestone

Figure

1, 2, 3, 4, 5. Incomplete protaspis: exterior stereograph; anterior, left lateral, antero-dorsal, postero-dorsal views, X 33.6. Photographs by W. R. Evitt. Locality 4. Original of Text-figure 11A.

6. Stage 0 cranidium and free cheek: exterior stereograph, X 30. Locality 4. Original of Text-figure 11B.

7. Same cranidium as figure 6.: interior view, X 30. Locality 4.

8, 11. Small cranidium: exterior stereograph; interior view, X 30. Locality 4. Original of Text-figure 11C.

9. Small free cheek: oblique exterior view, X 30. Locality 4. Original of Text-figure 11C.

10. Stage 0 pygidium: dorsal view, X 30. Locality 4. Original of Text-figure 11B.

12. Small cranidium and free cheek: exterior stereograph, X 30. Locality 3. Original of Text-figure 11D.

13. Transitory pygidium: dorsal view, X 30. Locality 4.

14. Small cranidium and free cheek: exterior stereograph, X 25. Locality 2. Original of Text-figure 11E.

15. Small cranidium and free cheek: exterior stereograph, X 15. Locality 2. Original of Text-figure 11F.

16, 17, 18. Small cranidium: dorsal, right lateral, anterior views, X 9. Locality 2.

19. Same cranidium as figure 14: interior view, X 20. Locality 2.

20. Transitory pygidium: dorsal view, X 30. Locality 4.

21, 22. Paratype free cheek: oblique interior views, X 15. USNM 116520a. Locality 2.

Plate 7

Diacanthaspis secretus n.sp.
Lower Edinburg limestone

Figure

1, 3, 5, 11. Holotype cranidium: dorsal and anterior views, X 9; interior view, X 6; left lateral view, X 9. USNM 116519. Locality 2.

2, 7. Paratype free cheek: dorsal and oblique exterior views, X 10. USNM 116520a. Locality 2.

4. Paratype thoracic segment: dorsal view, X 6. USNM 116520b. Locality 2.

6. Paratype, incomplete thoracic segment: dorsal view, X 6. USNM 116520b. Locality 2.

8. Pygidium: interior view, X 9. Locality 2.

9. Pygidium: dorsal view, X 9. Locality 4.

10. Paratype pygidium: dorsal stereograph, X 9. USNM 116520c. Locality 2.

12. Pygidium, exterior view, tips of border spines showing openings, X 30. Locality 2.

13, 14. Free cheek: oblique exterior views, border spines and librigenal spine showing openings, X 30. Locality 2.

Diacanthaspis lepidus n.sp.
Lower Edinburg limestone

15. Cranidium: anterior view to show spines X 30. Locality 2.

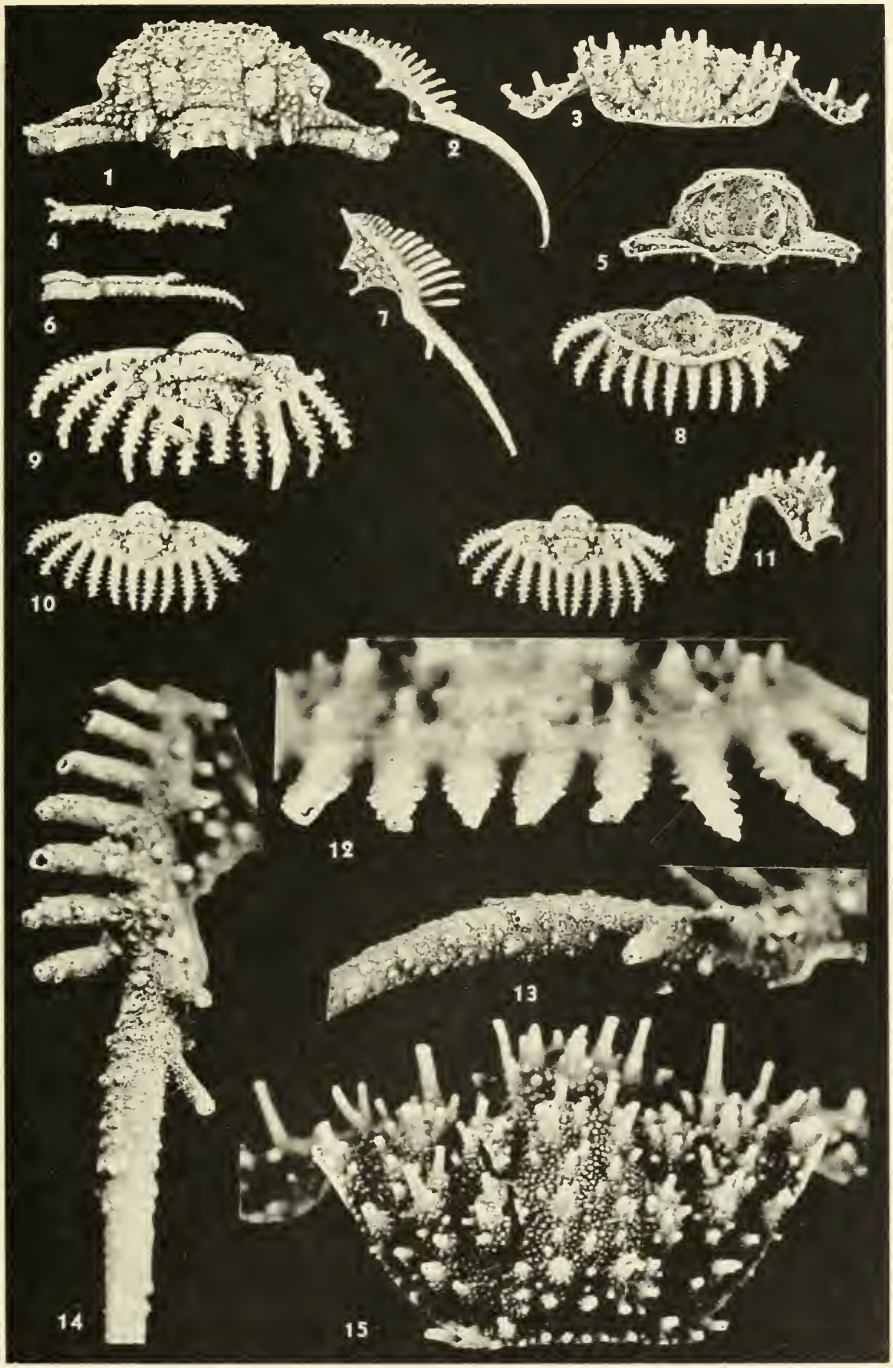
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PLATE 8

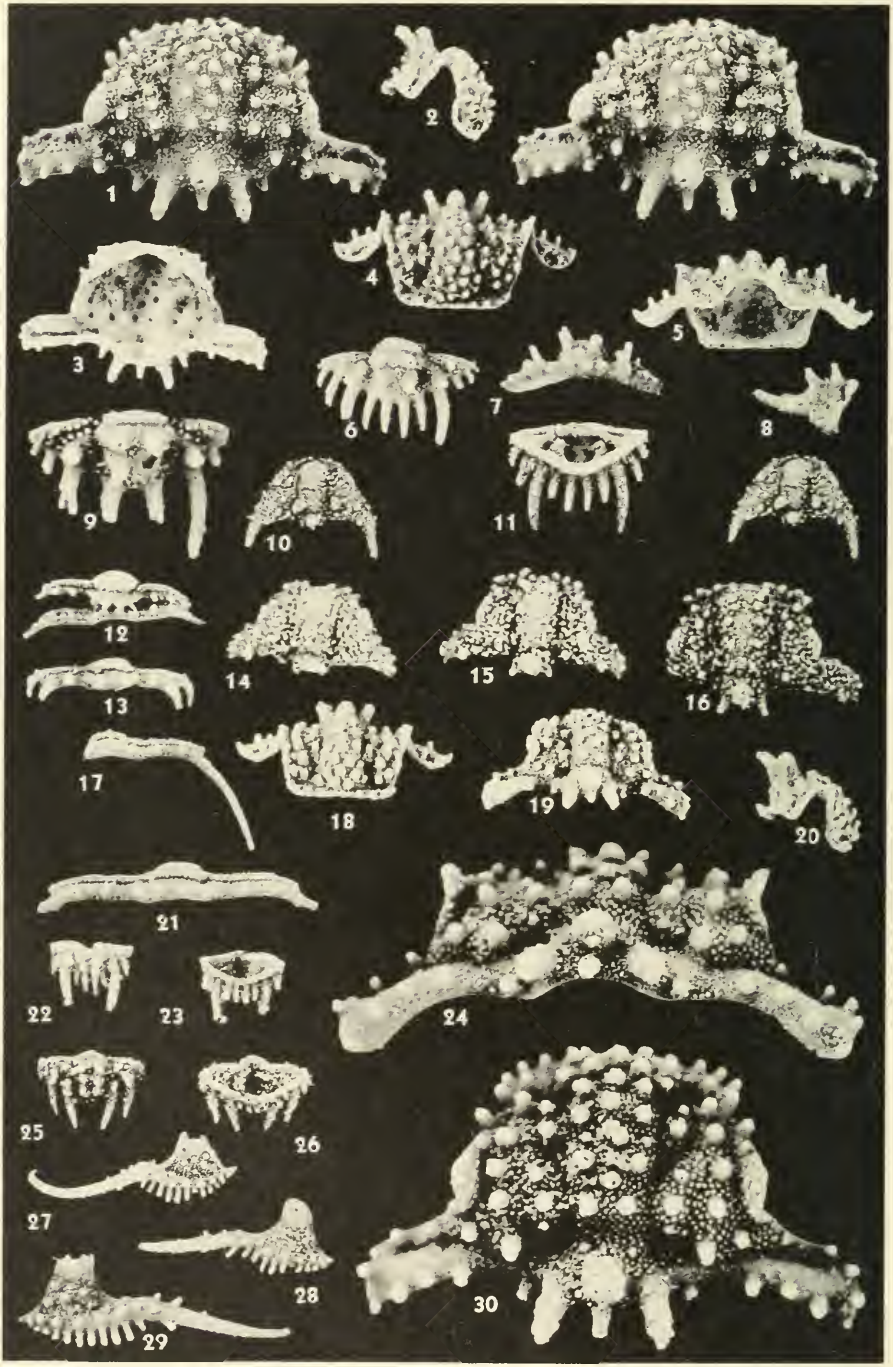
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Plate 8

Diacanthaspis ulrichi n.sp.
Lower Edinburg limestone

Figure

1, 2, 3, 4, 5. Holotype cranidium: dorsal stereograph, X 15; right lateral, interior, anterior, posterior views, X 10. USNM 116521. Locality 7.

6, 7, 8. Paratype pygidium: dorsal, posterior, right lateral views, X 15. USNM 116522c. Locality 7.

9. Pygidium: dorsal view, X 30. Locality 7.

10. Stage 0 cranidium: exterior stereograph, X 30. Locality 4. Original of Text-figure 12A.

11. Pygidium: ventral view, X 20. Locality 7.

12. Two paratype segments from anterior part of thorax: exterior view, X 15. USNM 116522b. Locality 7.

13. Paratype thoracic segment: dorsal view, X 15. USNM 116522b. Locality 7.

14. Small cranidium: exterior view, X 30. Locality 4. Original of Text-figure 12B.

15. Small cranidium: exterior view, X 30. Locality 4. Original of Text-figure 12C.

16. Small cranidium: exterior view, X 30. Locality 4. Original of Text-figure 12D.

17. Paratype thoracic segment: dorsal view, X 15. USNM 116522c. Locality 7.

18, 19, 20. Small cranidium: anterior, dorsal, right lateral views, X 15. Locality 4.

21. Paratype thoracic segment: dorsal view, X 15. USNM 116522b. Locality 7.

22, 23. Small pygidium: exterior and interior views, X 20. Locality 7.

24, 30. Cranidium: two exterior views to show spines and depressions at tip of occipital spine, X 30. Locality 7.

25, 26. Transitory pygidium: exterior and interior views, X 20. Locality 7.

27. Free cheek: oblique exterior view, X 9. Locality 7.

28. Small free cheek: oblique exterior view, X 30. Locality 7. Original of Text-figure 12D.

29. Free cheek: oblique exterior view, X 30. Locality 7.

Plate 9

Diacanthaspis aff. *ulrichi* n.sp.
Oranda formation, locality 8

Figure

1-3, 7, 9. Cranidium: 1, 2, 3, exterior stereograph, dorsal and left lateral views, X 9; 7, oblique exterior view showing spines and granulation on external surface, X 30; 9, oblique exterior view showing pits in smooth tip of median occipital spine, spines and granulation on external surface, X 30.

4, 8. Incomplete cranidium: 4, exterior stereograph, X 9; 8, exterior view showing pits in the smooth tip of median occipital spine, X 30.

5. Pygidium: dorsal stereograph, X 15.

Diacanthaspis cooperi Whittington
Lower Martinsburg shale, locality 10

6. Incomplete cranidium: exterior view showing openings in tips of spines and granulation, X 30.

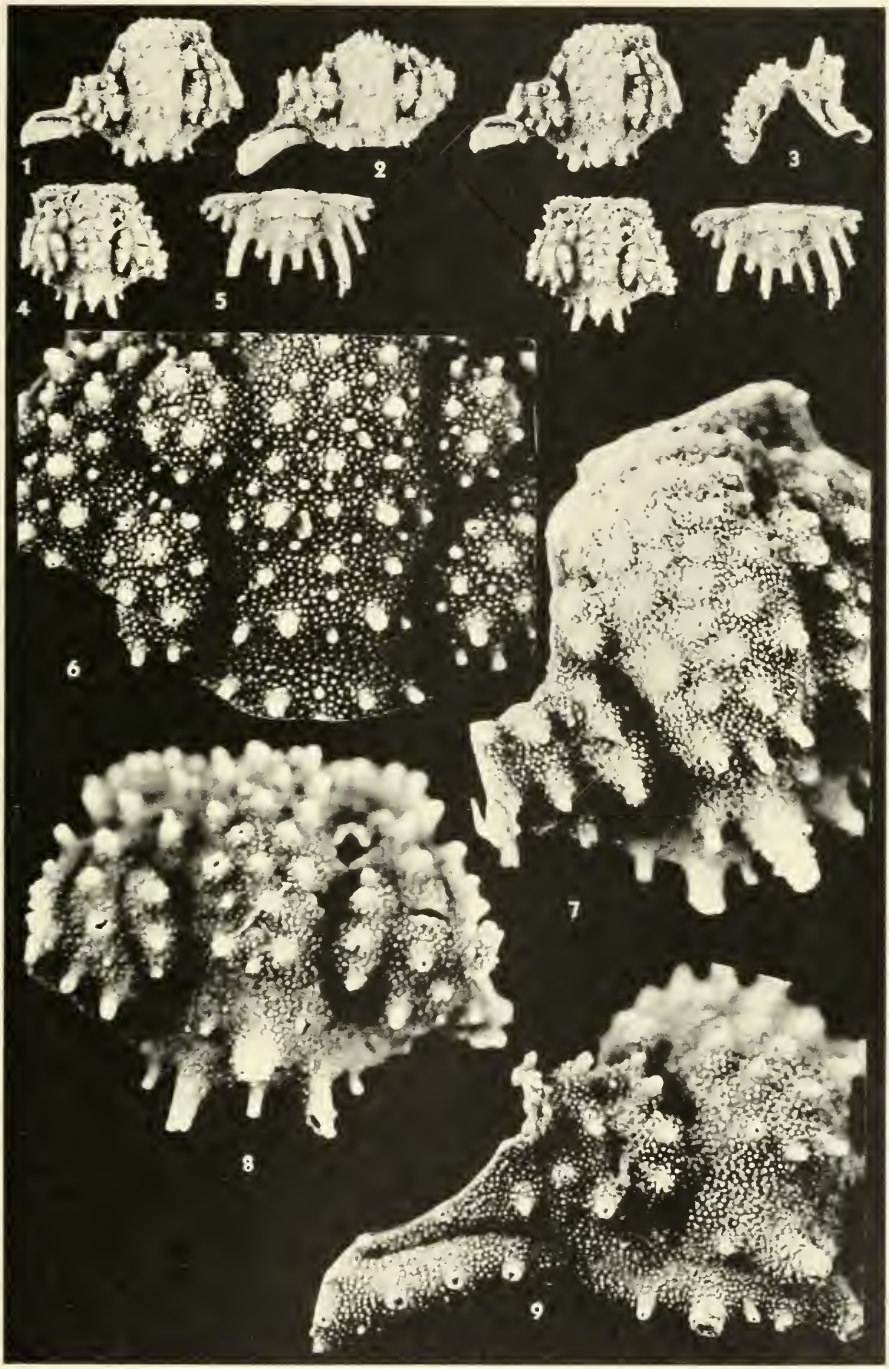
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PLATE 10

Plate 10

Diacanthaspis orandensis n.sp.
Oranda formation, locality 8

Figure

1, 3, 5-7. Holotype cranidium: exterior stereograph, dorsal, anterior, left lateral, posterior views, X 9. USNM 116523.

2, 4, 20. Paratype free cheek: oblique exterior, dorsal, and oblique interior views, X 9. USNM 116524a.

8-12. Paratype segment from anterior part of thorax: dorsal, ventral, posterior, anterior, right lateral views, X 10. USNM 116524c.

13, 14. Cranidium: interior and dorsal views, X 9.

15. Paratype segment from posterior part of thorax: dorsal view, X 15. USNM 116524d.

16. Paratype, right pleura of segment from posterior part of thorax, dorsal view, X 15. USNM 116524e.

17. Incomplete pygidium, dorsal view, X 9.

18. Incomplete pygidium, dorsal view, X 9.

19. Incomplete pygidium, dorsal view, X 9.

21-24. Paratype hypostome: interior, exterior, posterior, right lateral views, X 15. USNM 116524b.

25. Incomplete pygidium, ventral view, X 6.

26, 27. Paratype pygidium: 26, posterior view, X 6; 27, dorsal stereograph, X 9. USNM 116524f.

Plate 11

Diacanthaspis orandensis n.sp.
Oranda formation, locality 8

Figure

1. Smallest cranidium; exterior view, X 30.

2, 3. Small hypostome: interior, exterior views, X 20.

4. Paratype free cheek (original of Plate 10, figures 2, 4, and 20): oblique exterior view, X 9. USNM 116524a.

5. Small cranidium: exterior view, X 30.

6. Small free cheek: oblique exterior view, X 10.

7. Small cranidium: exterior view, X 30.

8. Pygidium (original of Plate 10, figure 18): posterior view, X 6.

9. Small pygidium: exterior view, X 20.

10. Small cranidium: exterior view, X 15.

11. Small cranidium: interior view, X 15.

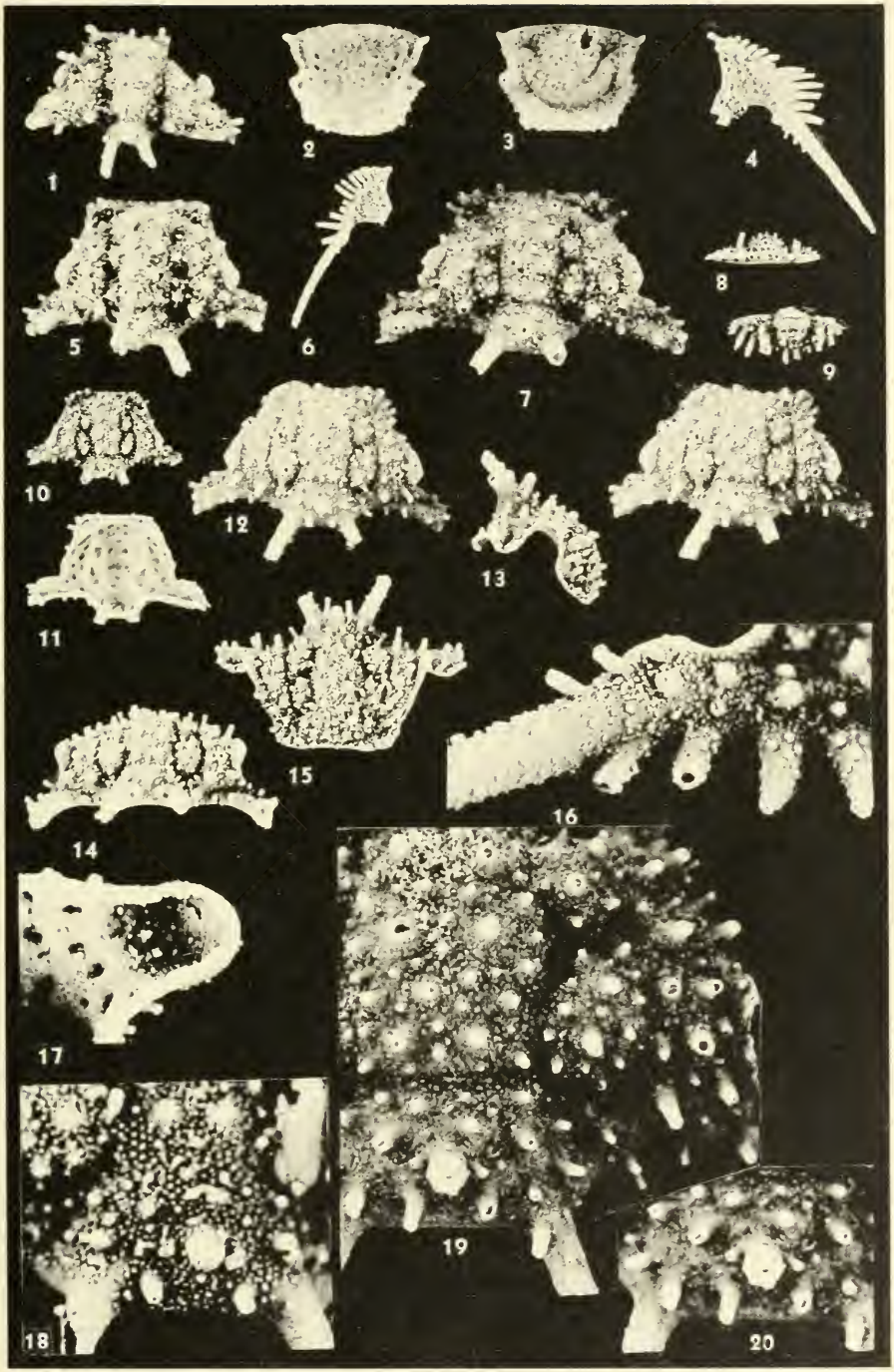
12-15. Small cranidium: exterior stereograph; right lateral, dorsal, anterior views, X 15.

19, 20. Incomplete cranidium: 19, exterior view of part of external surface; on right fixed cheek rounded tips of spines show minute dark spots, the locii of depressions or openings, X 30; 20, exterior view of part of occipital ring, showing pits in tip of median spine, X 30.

Diacanthaspis cooperi Whittington
Lower Martinsburg shale

16, 17. Free cheek: 16, oblique exterior view of base of librigenal spine and adjacent border showing openings in tips of border spines, X 30; 17, oblique interior view of eye surface showing facets, X 30. Locality 9.

18. Postero-median part of incomplete cranidium showing pits in tip of median occipital spine, X 30. Locality 10.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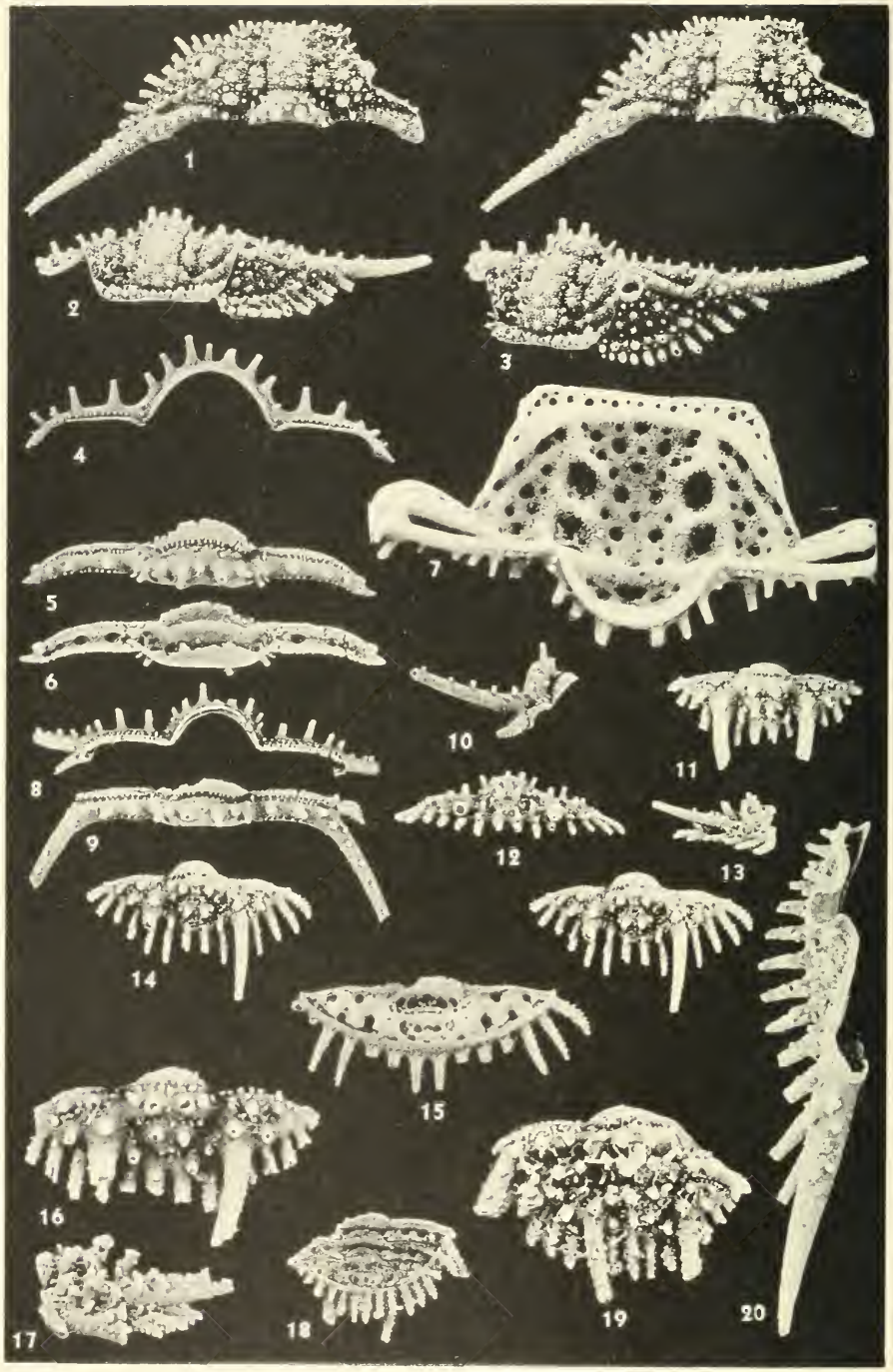
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Plate 12

Diacanthaspis scitulus n.sp.
Oranda formation, locality 8

Figure

1-3. Holotype cranidium and left free cheek: dorsal stereograph, anterior and antero-lateral views, X 9. USNM 116525.

4-6. Paratype segment from anterior part of thorax: posterior, dorsal, interior views, X 10. USNM 116526b.

7. Cranidium: interior view showing short third glabellar furrows, X 20.

8-10. Paratype segment from posterior part of thorax: anterior, dorsal, right lateral views, X 10. USNM 116526c.

11. Small pygidium: dorsal view, X 15.

12-14. Paratype pygidium: posterior, right lateral views, dorsal stereograph, X 9. USNM 116526e.

15. Pygidium: interior view, X 9.

16. Small pygidium: dorsal view, X 30.

17-19. Paratype, last two segments of thorax and pygidium: 17, left lateral view, X 15; 18, ventral view, X 10; 19, dorsal view, X 15. USNM 116526d.

20. Free cheek: oblique exterior view showing broad flattened edge along suture, X 15.

Plate 13

Diacanthaspis scitulus n.sp.
Oranda formation, locality 8

Figure

1, 2. Small cranidium: dorsal, anterior views, X 9.

3-5. Smallest known cranidium: dorsal, anterior, right lateral views, X 15.

6, 7. Free cheek showing injury: oblique interior and oblique exterior views, X 9.

8, 10, 11. Paratype hypostome: exterior stereograph, posterior and left lateral views, X 15. USNM 116526a.

9. Hypostome: interior stereograph, X 15.

12, 15. Paratype pygidium (original of Plate 12, figures 12-14): enlarged views of external surface to show tips of spines, X 30. USNM 116526e.

13. Small free cheek: oblique exterior view, X 30.

14. Free cheek, tip of librigenal spine showing openings in spines on external surface, X 30.

16, 17. Cranidium: 16, part of glabella, right fixed cheek and anterior border showing spines and granules, X 30; 17, part of fronto-median glabellar lobe showing minute openings in tips of paired axial spines, X 50.

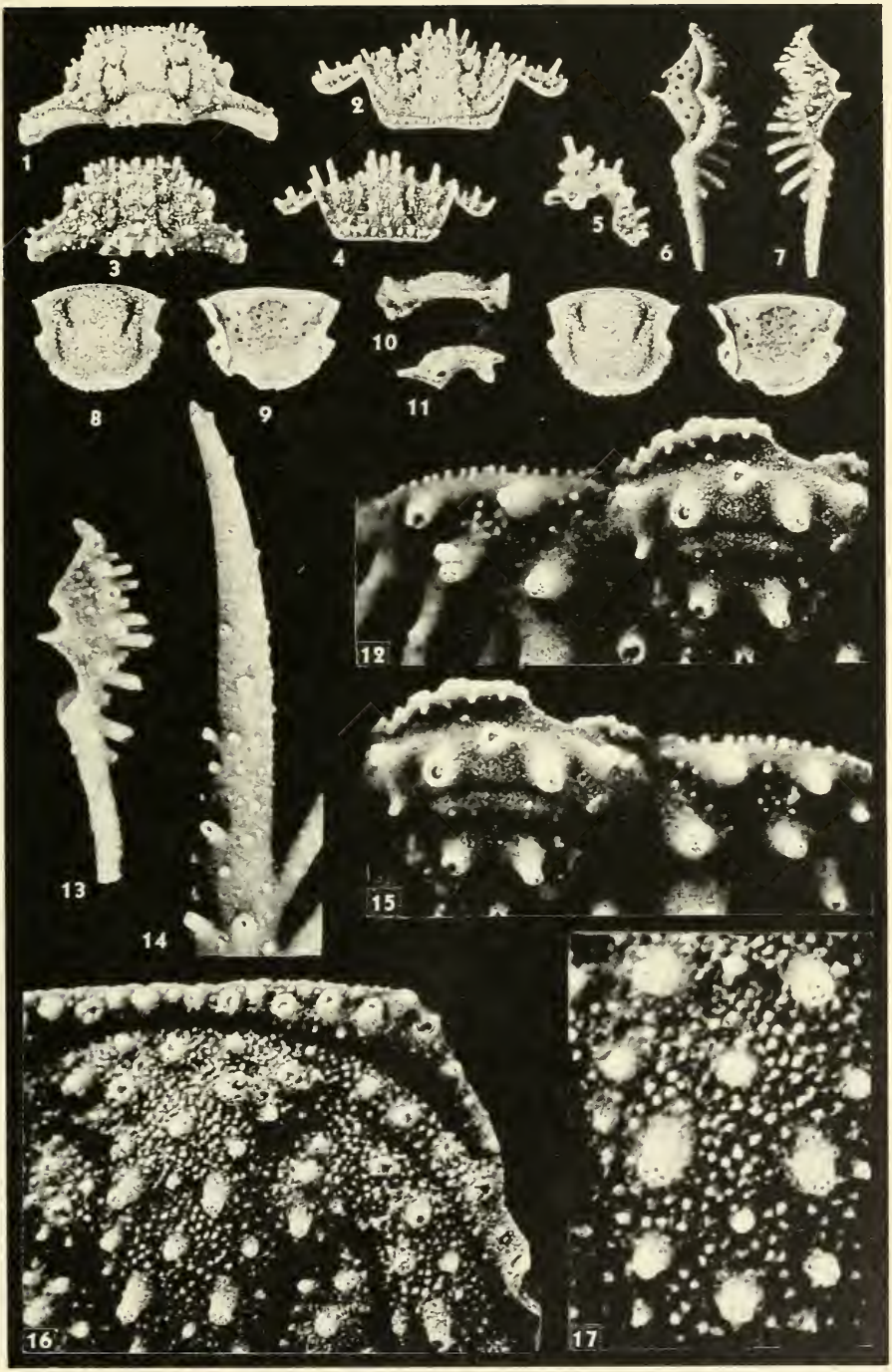
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PLATE 14

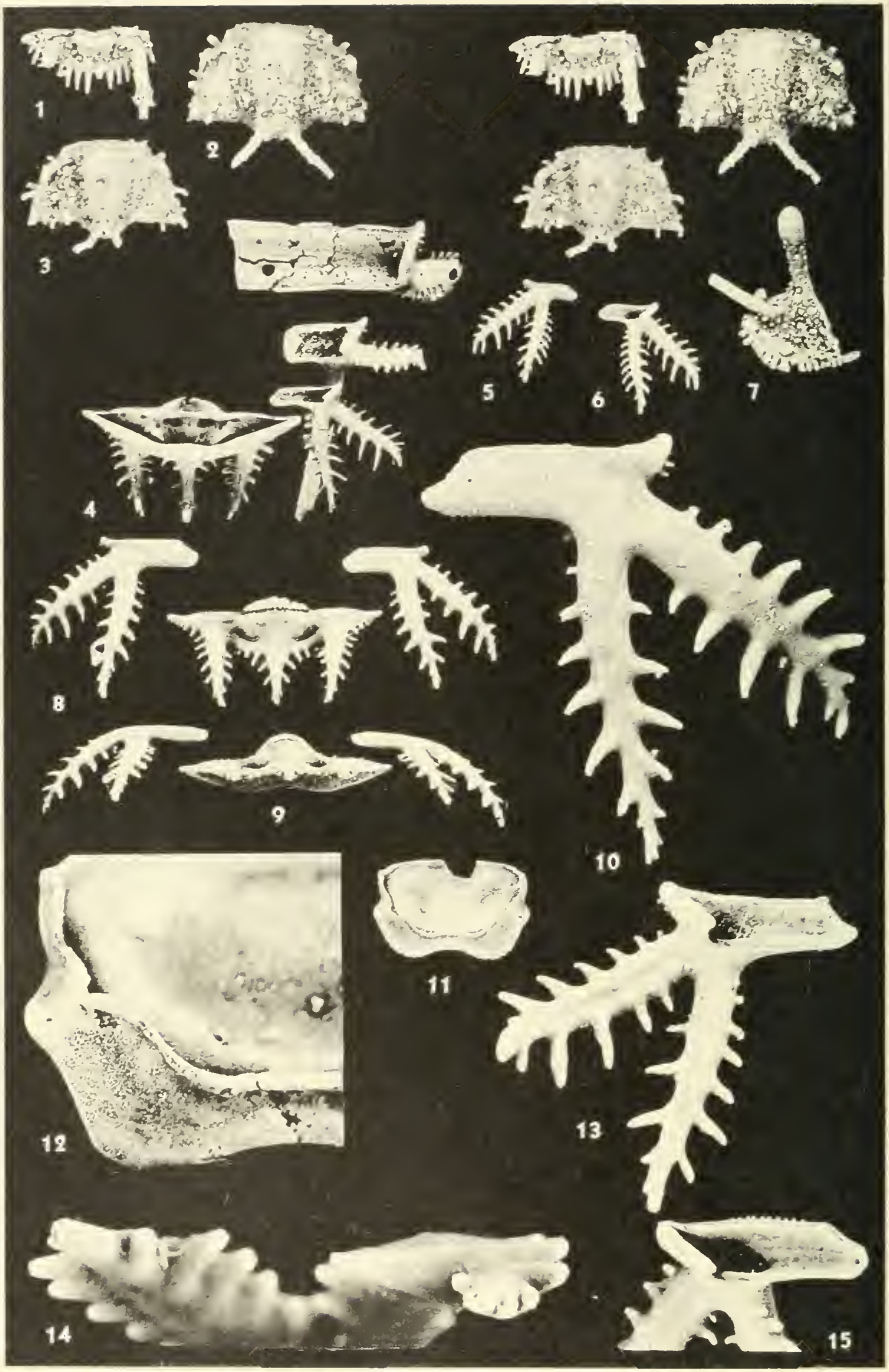

Plate 14

?Miraspis sp.ind.
Lower Edinburg formation, locality 3

Figure

1. Pygidium: dorsal stereograph, X 9.

7. Free cheek, oblique exterior view, X 9.
Ceratocephala laciniata Whittington and Evitt

2. Small cranidium: exterior stereograph, X 30.

3. Small cranidium: exterior stereograph, X 30. Original of Text-figure 16.

4. Outer parts of pleurae of two posterior thoracic segments, pygidium, and objects of uncertain affinities (pin supporting this object not blacked out) arranged in approximate relative positions: ventral view, X 6.

5, 6. Objects of uncertain affinities, smallest size known: exterior and interior views, X 10.

8, 9. Left- and right-hand objects of uncertain affinities, arranged in juxtaposition with a pygidium: dorsal and posterior views, X 6.

10. Objects of uncertain affinities: "dorsal" view, X 9.

11. Small hypostome: interior view showing tiny opening through doublure at shoulder, X 10.

12. Paratype hypostome (original of Whittington and Evitt, 1954, Pl. 6, figs. 10-13): enlarged view of part of interior, showing openings through doublure at shoulder, X 20. USNM 116503c.

13. Object of uncertain affinities: "ventral" view showing posterior edge of "pleura" X 10.

14, 15. Objects of uncertain affinities: 14, tips of "pleural" spines showing openings at tips of barbs, X 30; 15, oblique interior view showing anterior and inner edges of "pleura" X 15.

Plate 15

Ceratocephala rarispina n.sp.
Oranda formation, locality 8

Figure

1, 4, 5, 7. Holotype cranidium: exterior stereograph, anterior, interior and dorsal views, X 9. USNM 116527.

2, 12. Paratype free cheek: exterior and right lateral views, X 9. USNM 124698a.

3, 6, 8. Fragment of left side of cranidium with incomplete free cheek attached, showing course of suture and poorly preserved eye lobe: oblique exterior, exterior, and anterior views, X 9.

9. Pleural portion of segment from anterior part of thorax: dorsal view, X 9

10, 13. Paratype segment from anterior part of thorax: posterior and dorsal views, X 9. USNM 124698c.

11, 14-16. Cranidium: left lateral, anterior, posterior, exterior views, X 10.

17. Incomplete segment from posterior part of thorax: dorsal view, X 9.

18, 20, 21. Paratype pygidium: dorsal, posterior and left lateral views, X 15. USNM 124698d

19. Pygidium: dorsal view, X 30

22, 23. Paratype hypostome: interior and exterior views, X 30. USNM 124698b.

24. Small cranidium and left free cheek: exterior stereograph, X 20.

25, 28. Cranidium, incomplete but showing entire anterior border (compare with Figure 1): 25, exterior view, X 10; 28, part of axial region showing depressions (appearing as dark spots) in tips of spines, X 30.

29. Free cheek: oblique exterior view, X 20.

Ceratocephala (*Ceratocephalina* n.subgen.) sp.ind.
Lower Edinburg formation, locality 4.

26, 27, 30. Cranidium: anterior, right lateral, dorsal views, X 15.

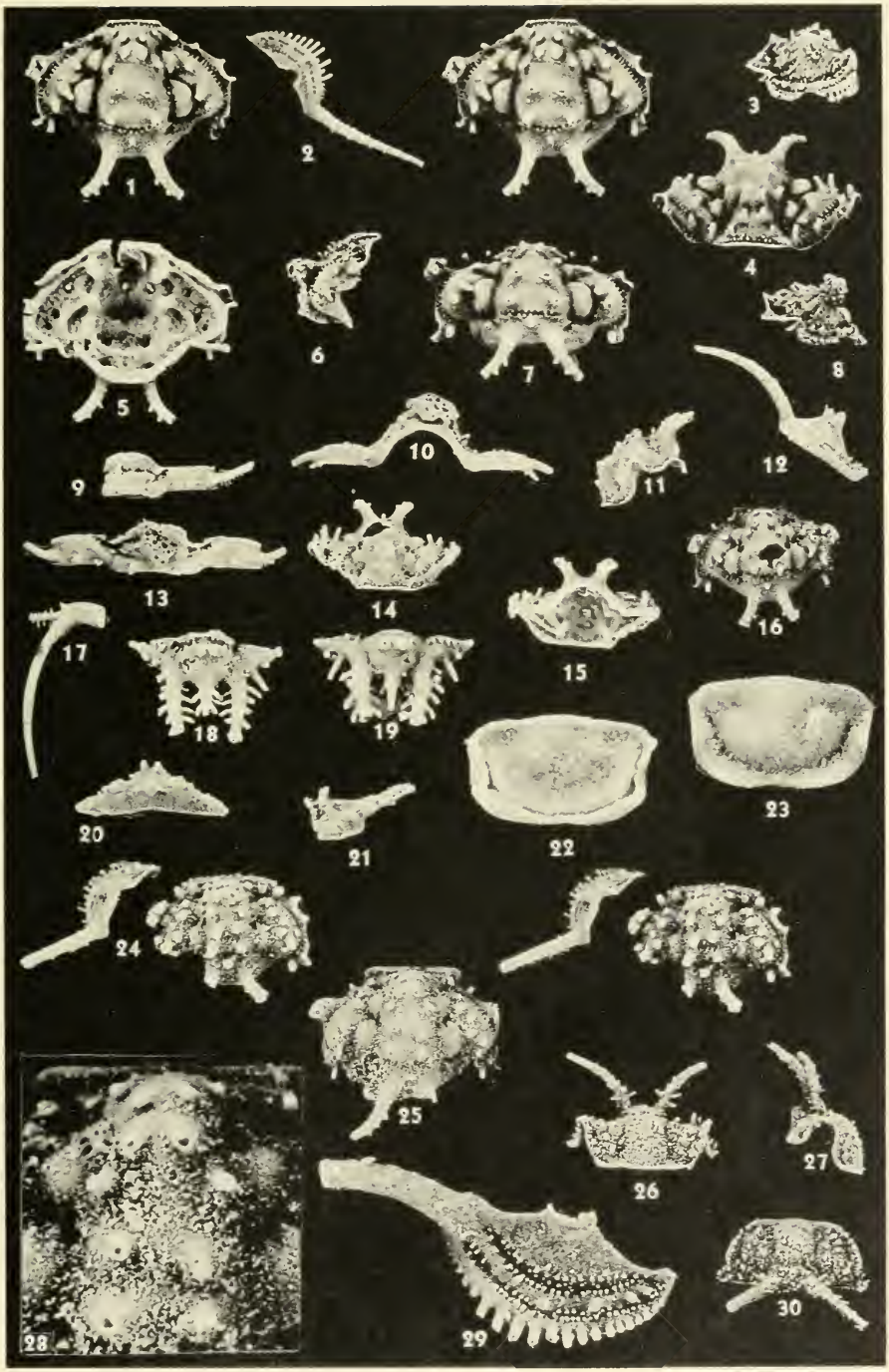
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PLATE 16

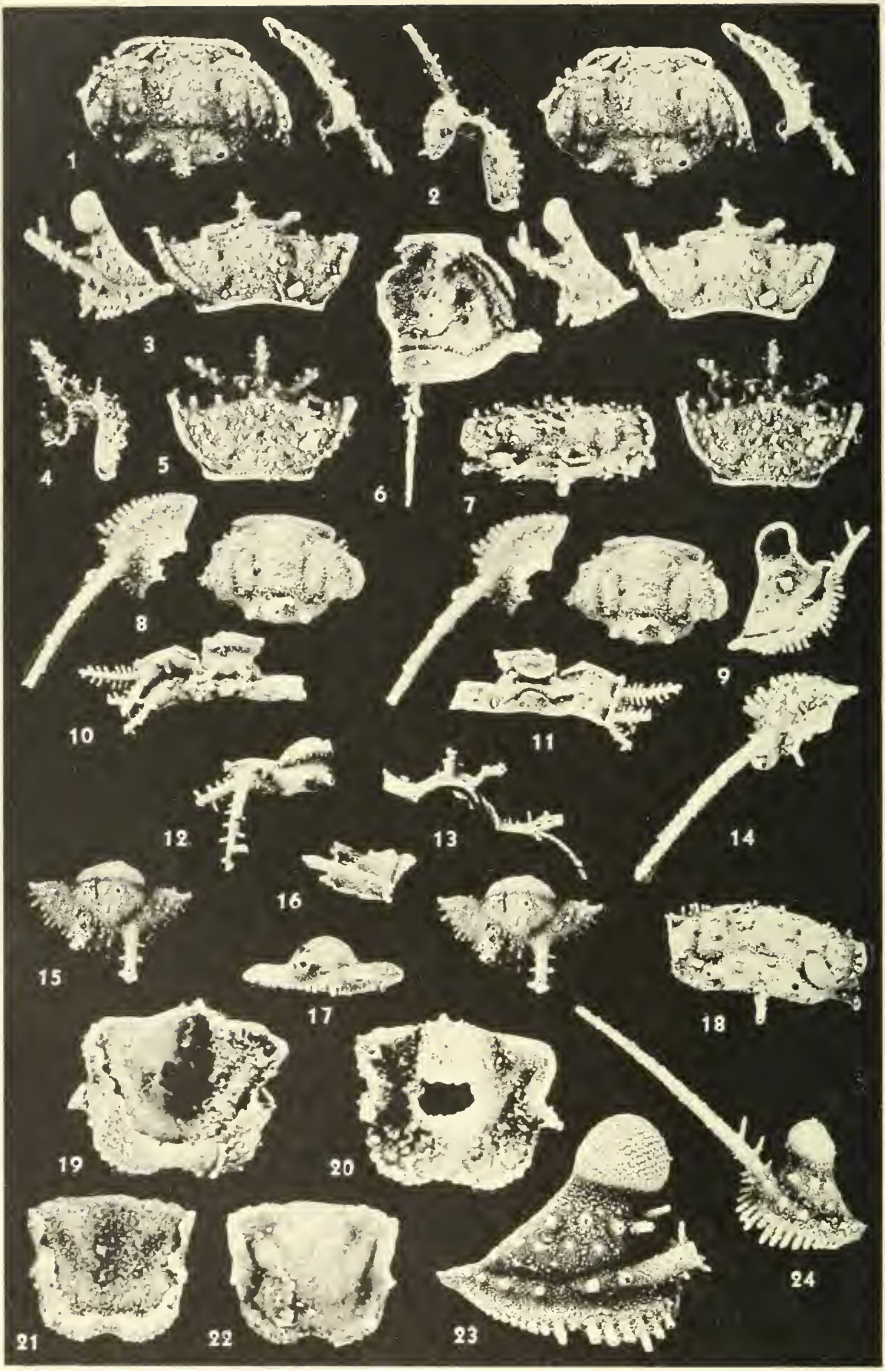


Plate 16

Ceratocephala (*Ceratocephalina*) *tridens* n.subgen., n.sp.
Lower Edinburg limestone

Figure

1, 3. Holotype cranidium and paratype free cheek: exterior and anterior stereographs, X 9. Locality 4. USNM 124699, 124700a.

2, 18. Holotype cranidium: right lateral and dorsal views, X 9. Locality 4. USNM 124699. Ostracod carapace adhering to base of glabella on right side (figure 18) was removed before photographs forming figures 1-3 were made.

4, 5, 7. Cranidium: right lateral view, anterior stereograph, dorsal view, X 9. Locality 4.

6. Incomplete cranidium: interior view, X 10. Locality 4.

8. Small cranidium and free cheek: exterior stereograph, X 20. Locality 4.

9. Paratype free cheek: oblique interior view, X 9. Locality 4. USNM 124700a.

10, 11, 13. Paratype, 2 thoracic segments: dorsal, ventral and anterior views, X 9. Locality 4, USNM 124700b.

12. Paratype thoracic segment: dorsal view, X 9. Locality 4. USNM 124700b.

14. Small free cheek: oblique exterior view, X 30. Locality 4.

15-17. Paratype pygidium: dorsal stereograph, right lateral, posterior views, X 15. Locality 4. USNM 124700c.

19, 20. Hypostome: interior and exterior views, X 30. Locality 4.

21, 22. Hypostome: interior and exterior views, X 30. Locality 4.

23. Free cheek: oblique exterior view showing eye surface, X 20. Locality 3.

24. Free cheek: oblique exterior view, X 20. Locality 4.

Plate 17

Apianurus barbatus n.gen., n.sp.
Lower Edinburg limestone

Figure

1, 16. Paratype free cheek: exterior and left lateral views, X 4. Locality 2, USNM 124702a.

2. Cranidium: exterior stereograph, X 4. Locality 3.

3, 4, 6. Holotype cranidium: exterior stereograph, dorsal and left lateral views, X 4. Locality 2, USNM 124701.

5, 7, 9-11. Cranidium from Locality 2, free cheek from locality 3: anterior view, antero-lateral stereograph, right lateral view, left antero-lateral view, dorsal stereograph, X 4.

8,212. Cranidium: posterior and interior views, X 4. Locality 3.

13. Right free cheek: lateral view, X 9. Locality 2.

14. Left free cheek: exterior view, X 9. Locality 2.

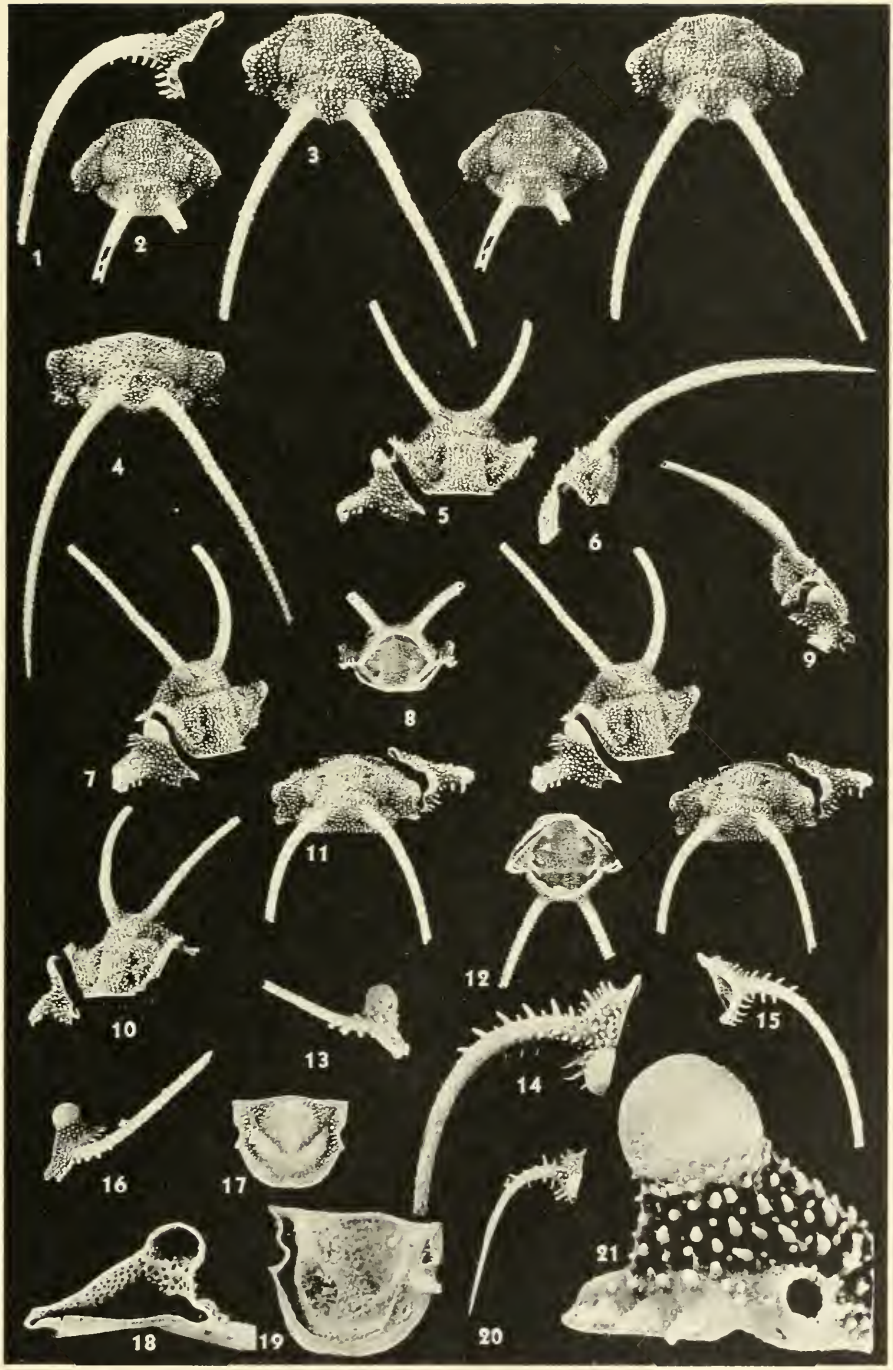
15. Left free cheek: ventral view, X 4. Locality 3.

17, 19. Hypostome: exterior view, oblique interior view showing opening through doublure at shoulder and posterior wing, X 9. Locality 2.

18. Free cheek: interior view, X 6. Locality 3.

20. Free cheek with complete librigenal spine: dorsal view, X 6. Locality 2.

21. Right free cheek: exterior view showing eye surface, X 30. Locality 2.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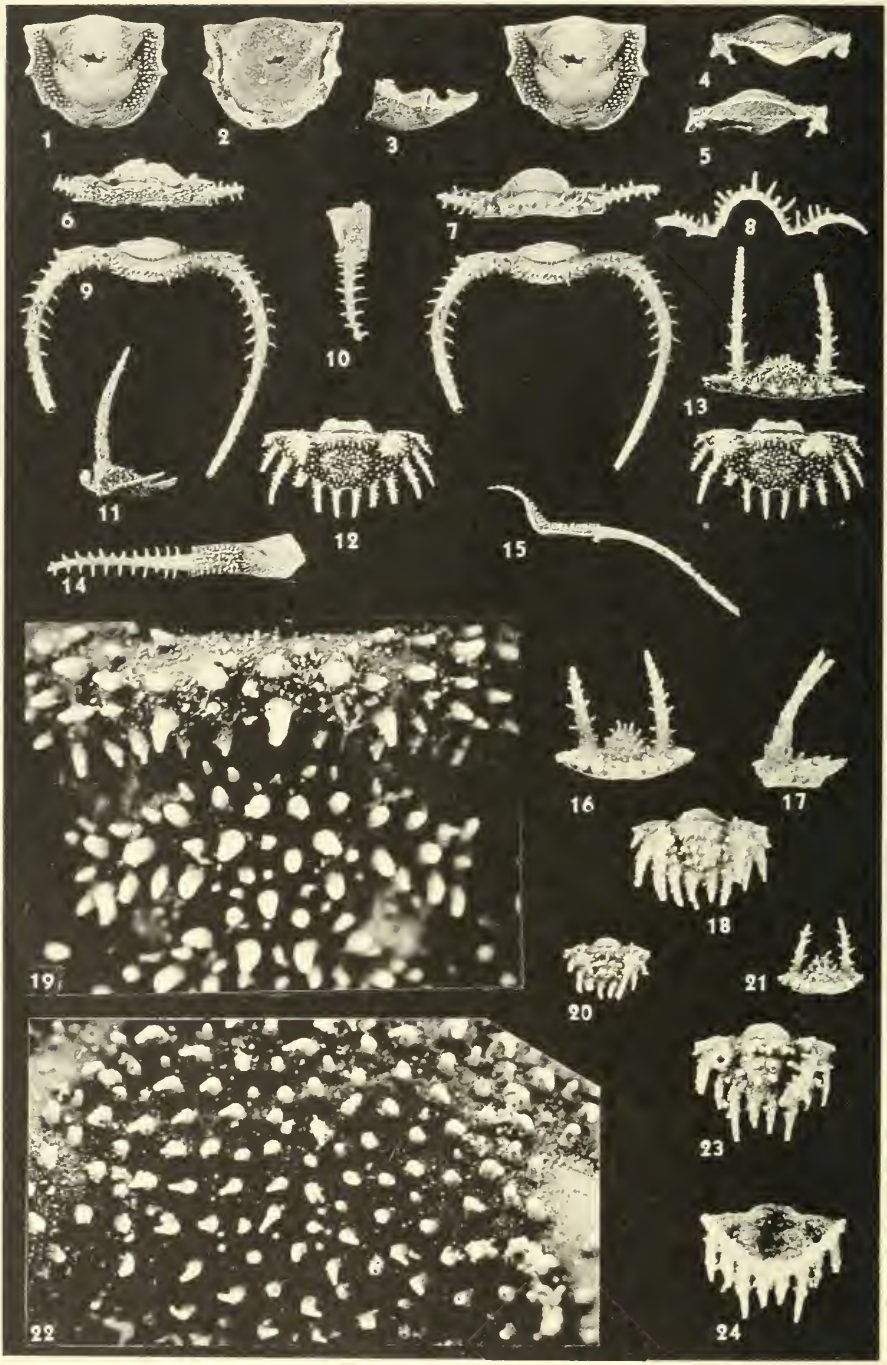
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Plate 18

Apianurus barbatus n.gen., n.sp.
Lower Edinburg limestone

Figure

1-5. Paratype hypostome: exterior stereograph, interior, left lateral, posterior, anterior views, X 4. Locality 2. USNM 124702b.

6. Paratype anterior thoracic segment: dorsal view, X 4. Locality 2. USNM 124702d.

7, 8. Anterior thoracic segment: dorsal and posterior views, X 10. Locality 2.

9. Paratype thoracic segment: dorsal stereograph, X 4. Locality 2. USNM 124702c.

10, 14, 15. Paratype incomplete thoracic segment: left lateral, dorsal, anterior views, X 4. Locality 2. USNM 124702d.

11-13. Paratype pygidium: left lateral view, dorsal stereograph, posterior view, X 4. Locality 2. USNM 124702e.

16-18. Small pygidium: posterior, left lateral, dorsal views, X 10. Locality 2.

19. Pygidium: enlarged view of anterior part of axis showing spines on external surface, X 30. Locality 2.

20, 21. Small pygidium: dorsal and posterior views, X 10. Locality 2.

22. Cranidium: enlarged view of median part of occipital ring between occipital spines showing external surface, X 30. Locality 2.

23, 24. Small holaspid pygidium: dorsal and ventral views, X 30. Locality 4.

Plate 19

Apianurus barbatus n.gen., n.sp.
Lower Edinburg limestone

Figure

1, 3. Stage 0 free cheek: exterior and interior views, X 30. Locality 4. Original of Text-figure 22A.

2. Stage 0 cranidium: exterior stereograph, X 30. Locality 3. Original of Text-figure 22A.

4, 6. Stage 0 (?) cranidium lacking right fixigenal spine, exterior and interior views, X 30. Locality 4.

5. Stage 0 transitory pygidium: exterior stereograph, X 30. Locality 4. Original of Text-figure 22A.

7. Small cranidium: exterior view, X 30. Locality 2. Original of Text-figure 22C.

8. Small free cheek: exterior view, X 30. Locality 4. Original of Text-figure 22C.

9, 10. Small cranidium: exterior and interior views, X 30. Locality 3. Original of Text-figure 22B.

11. Small free cheek: exterior view, X 15. Locality 4. Original of Text-figure 22D.

12, 13. Small hypostome: exterior and interior views, X 30. Locality 3.

14 16. Small cranidium: dorsal, anterior, right lateral views, X 15. Locality 2.

17, 21. Small hypostome: exterior and interior views, X 30. Locality 3.

18 20. Small cranidium: dorsal, anterior and left lateral views, X 10. Locality 2.

22, 23. Small cranidium: exterior and left lateral views, X 15. Locality 2.

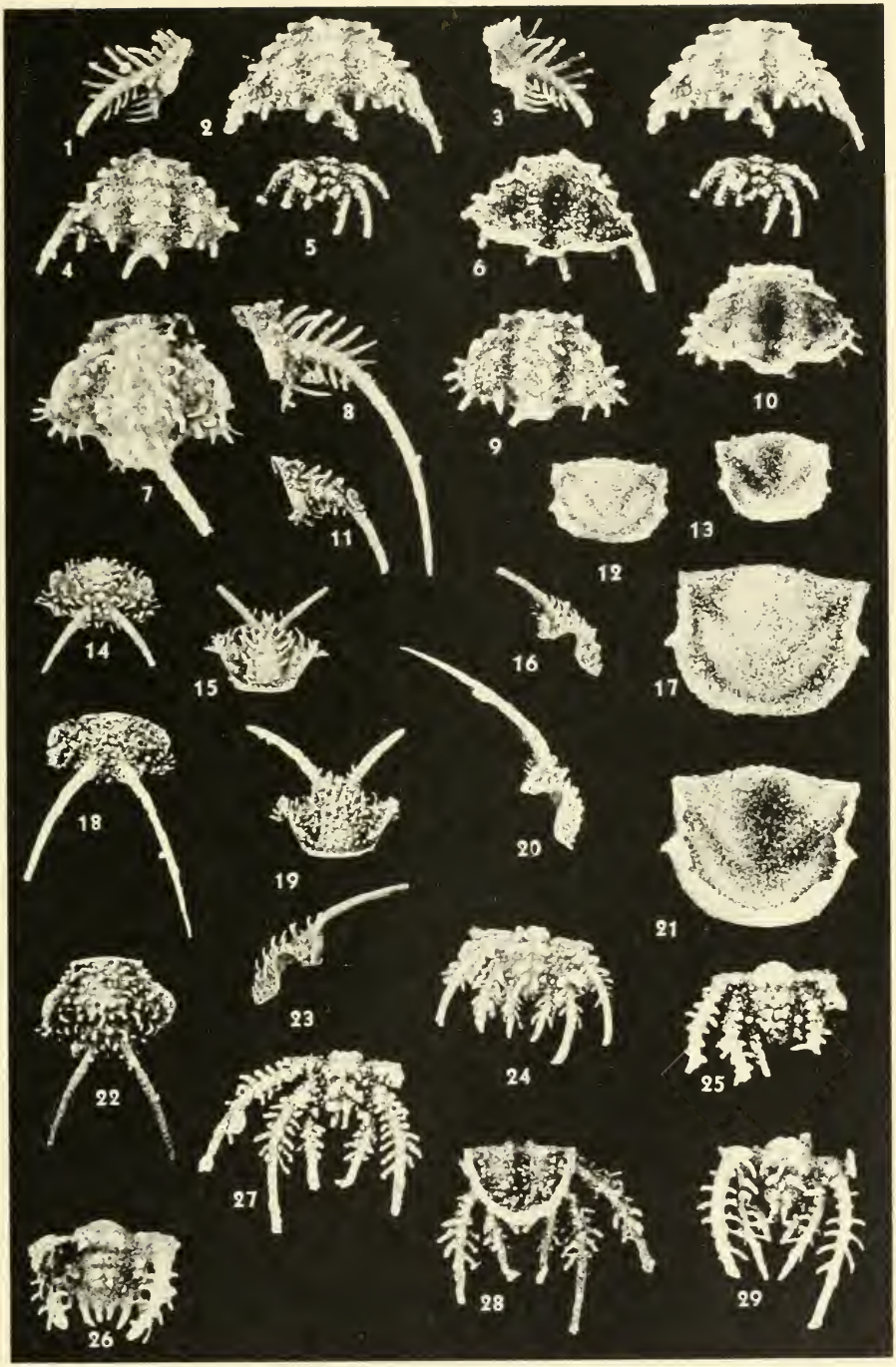
24. Transitory pygidium: dorsal view, X 30. Locality 4.

25. Transitory pygidium: dorsal view, X 30. Locality 4.

26. Transitory pygidium, Stage holaspis-1; dorsal view, X 30. Locality 2.

27, 28. Transitory pygidium: dorsal and ventral views, X 30. Locality 4.

29. Transitory pygidium: dorsal view, X 30. Locality 4.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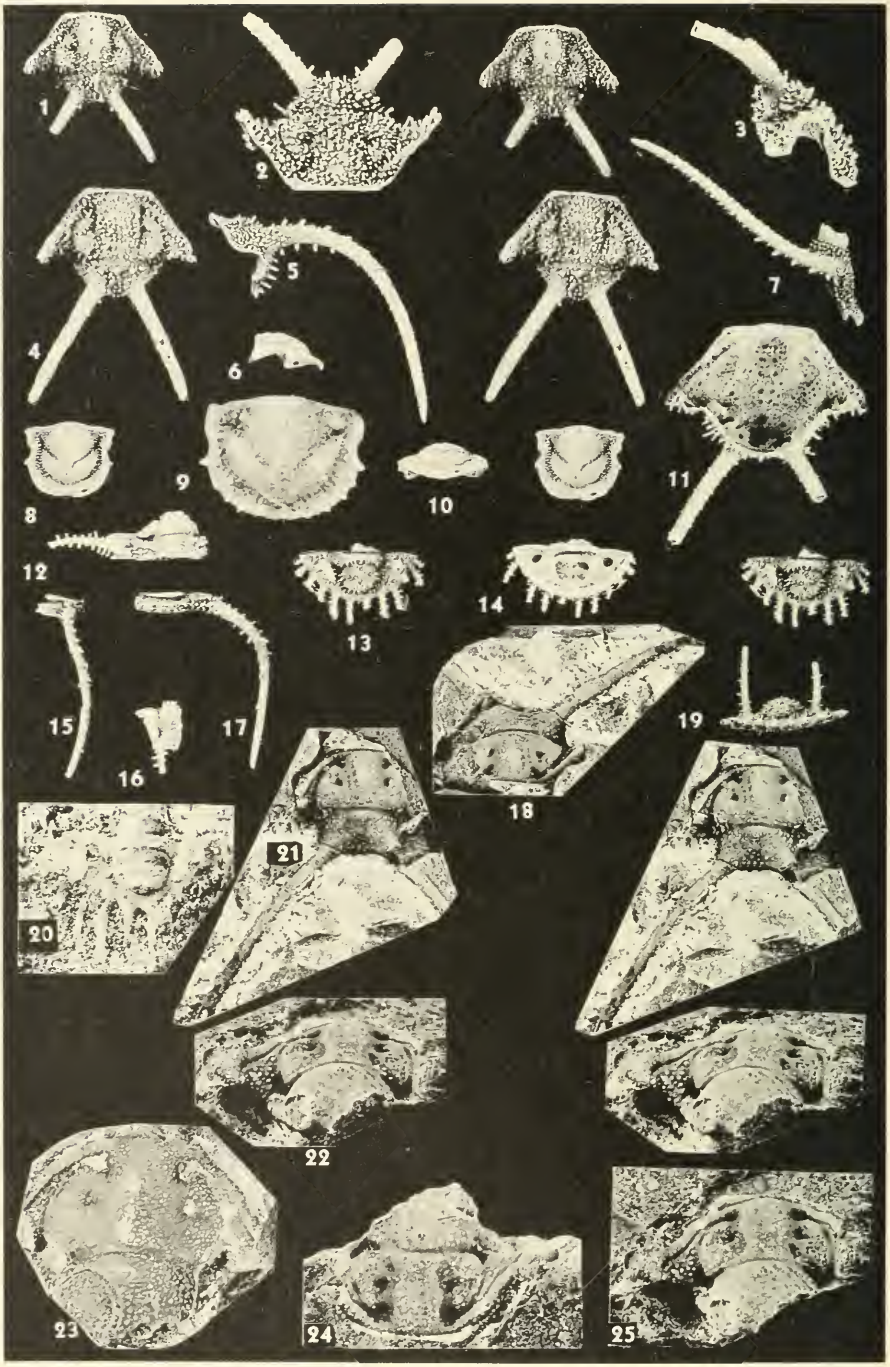
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Plate 20

Apianurus barbatus n.gen., n.sp.
Oranda formation, locality 8

Figure

1-3, 11. Cranidium: exterior stereograph, X 4; anterior, right lateral, and interior views, X 6.

4. Cranidium: exterior stereograph, X 6.

5, 7. Free cheek: dorsal and right lateral views, X 4.

6, 8, 10. Hypostome: right lateral view, exterior stereograph, posterior view, X 4.

9. Small hypostome: exterior view, X 30.

12, 16. Segment from anterior part of thorax: dorsal and left lateral views, X 4.

13, 14, 19. Pygidium: dorsal stereograph; ventral and posterior views, vieys, X 4.

15, 17. Segment from posterior part of thorax; right lateral and dorsal views, X 4.

Apianurus aff. *furcata* (Linnarsson)
Middle Ordovician, Chasmops limestone, southern Norway

18, 21. Incomplete cranidium: anterior view, exterior stereograph, X 2. Guttormsberget. PMO 66690.

20. Pygidium: dorsal view, X 10. Bygdøy. PMO 5647.

22, 24, 25. Incomplete cranidium: dorsal stereograph, anterior and exterior views, X 4. Guttormsberget. PMO 66691a.

23. Cranidium: exterior view, X 2.2 Fernholmen. PMO 3673.

Plate 21

Apianurus glaber n.gen., n.sp.
Lower Edinburg limestone, locality 2

Figure

1, 3. Holotype cranidium: exterior stereograph, right lateral, dorsal views, X 4. USNM 124703.

4, 5. Incomplete cranidium: dorsal and exterior views, X 4.

6, 7. Incomplete cranidium: interior and postero-lateral views, X 6.

8, 10. Paratype pygidium: posterior, right lateral and interior views, X 4. USNM 124704a.

11, 12. Incomplete cranidium: exterior and left lateral views, X 4.

13, 14. Paratype hypostome: interior view, exterior stereograph, X 6. USNM 124704b.

15. Pygidium: dorsal stereograph, X 4.

Apianurus sp.ind.
Lower Edinburg limestone, locality 2

16, 17, 19. Pygidium; dorsal stereograph, X 6; posterior and left lateral views, X 4. USNM 124705a.

18. Pygidium: dorsal stereograph, X 6. USNM 124705b.

20, 25. Hypostome: exterior stereograph, interior view, X 9. USNM 124705d.

21. Pygidium: dorsal view, X 15. USNM 124705c.

22, 26. Hypostome: interior and exterior views, X 9. USNM 124705e.

Odontopleurid protaspis, ? subfamily Miraspinae
Lower Edinburg limestone, locality 4

23, 24. Exterior stereograph, right lateral view, X 33.6. Photograph by W. R. Evitt.

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PLATE 22

Plate 22

Calipernurus insolitus n.gen., n.sp.
Lower Edinburg limestone

Figure

1-3, 6. Holotype, incomplete cephalon: exterior stereograph, left lateral, anterior, posterior views, X 9. Locality 3. USNM 124711.

4, 5, 7. Cranidium (Locality 3) and free cheek (Locality 2): dorsal and antero-lateral stereographs, exterior view, X 6.

Plate 23

Calipernurus insolitus n.gen., n.sp.
Lower Edinburg limestone

Figure

1, 3. Holotype, incomplete cephalon: ventral, dorsal views, X 9. Locality 3. USNM 124711.

2, 4. Cranidium (original of Plate 22, figures 4, 5, 7): posterior, interior views, X 4. Locality 3.

5, 7. Cranidium: dorsal and exterior views, X 9. Locality 3.

6. Tip of librigenal spine showing openings at base of barbs. X 30. Locality 3.

8. Cranidium; exterior view showing pits in median occipital tubercle, X 15. Locality 3.

9, 10. Free cheek (original of Plate 22, figures 4, 5 and 7); oblique interior and oblique exterior views of eye surface, X 30. Locality 2.

11, 12, 15. Paratype hypostome: exterior stereograph, X 6; interior view, X 6; oblique interior view, X 15 (arrow points to tiny opening in doublure). Locality 2. USNM 124712a.

13,14. Hypostome: exterior stereograph, interior view, X 9. Locality 2.

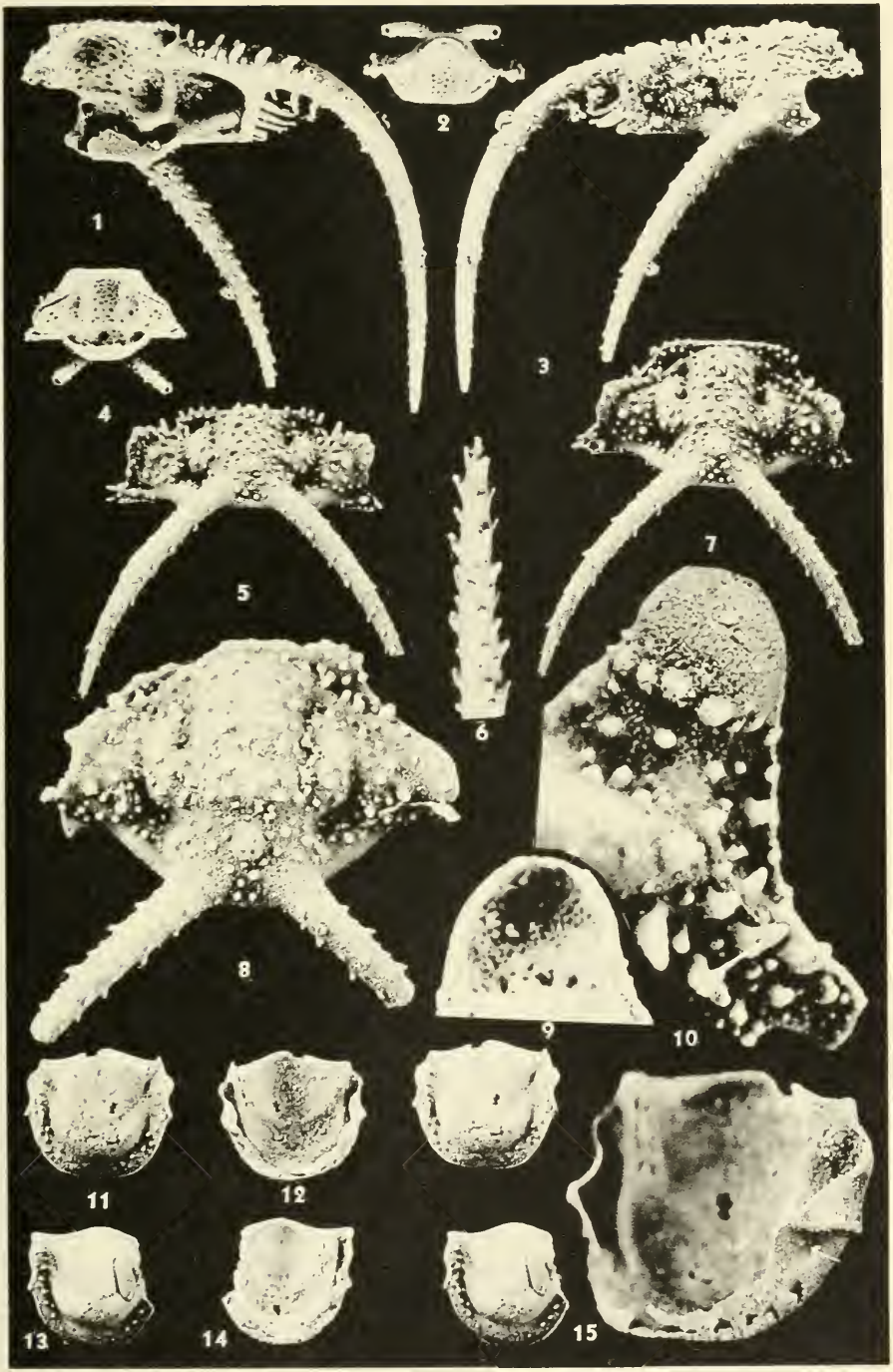
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PLATE 24

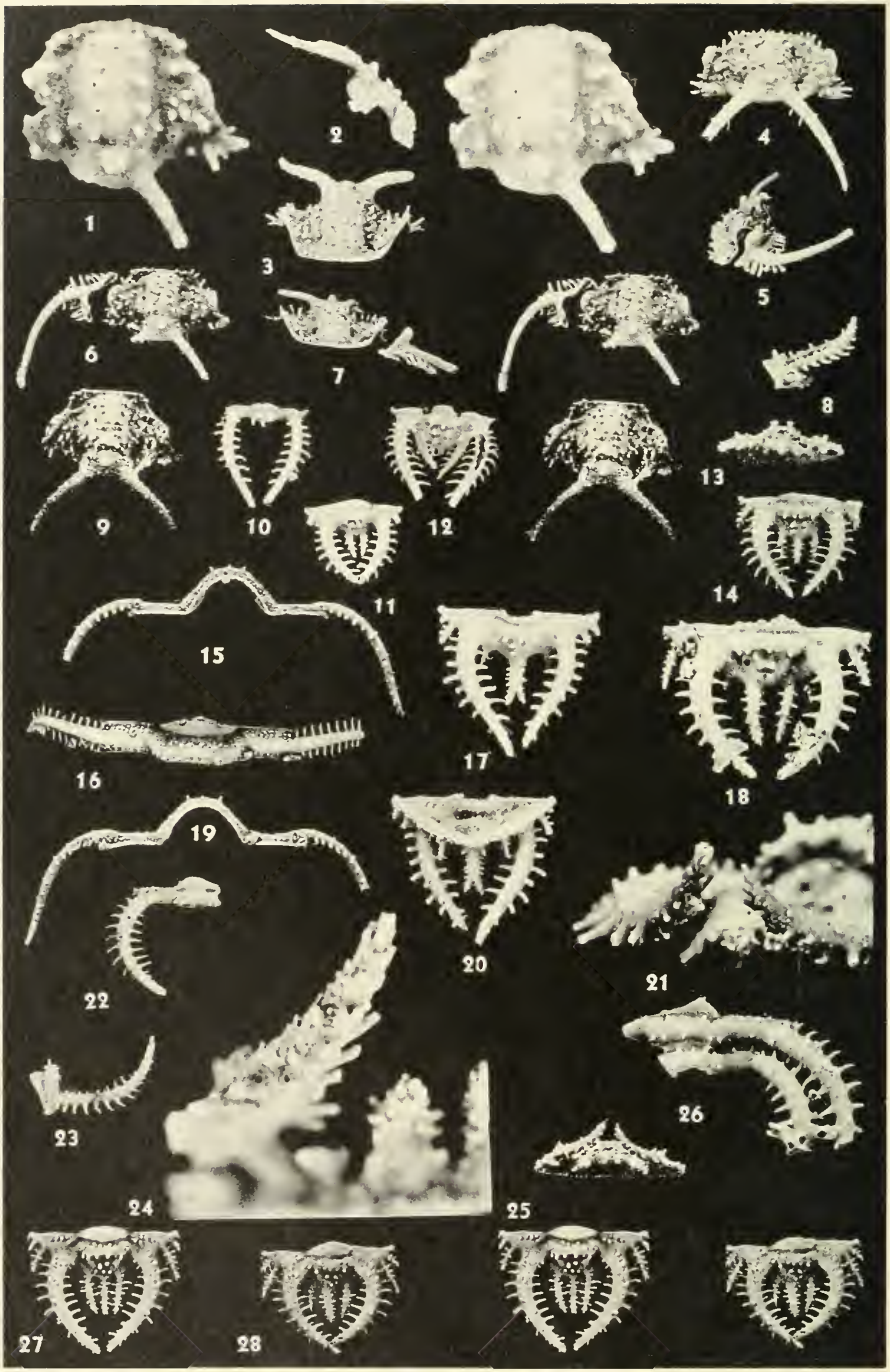

Plate 24

Calipernurus insolitus n.gen., n.sp.
Lower Edinburg limestone

Figure

1. Small cranidium: exterior stereograph, X 30. Locality 3.

2-4. Small cranidium: right lateral, anterior, dorsal views, X 10. Locality 2.

5-7. Small cranidium (Locality 2) and free cheek (Locality 3): left lateral view, exterior stereograph, anterior view, X 10.

8, 13, 14. Small pygidium: left lateral, posterior, dorsal views, X 1,. Locality 3.

9. Cranidium: exterior stereograph, X 10. Locality 2.

10. Small segment from posterior part of thorax: dorsal view, X 10. Locality 3.

11. Small pygidium lacking median border spine: dorsal view. X 12. Locality 3.

12. Transitory pygidium: dorsal view, X 15. Locality 2.

15, 16, 19. Paratype segment: anterior, dorsal, posterior views, X 4.5. Locality 3. USNM 124712b.

17, 20. Pygidium with median border spine distally bifurcated: dorsal and ventral views, X 10. Locality 3.

18. Pygidium lacking median border spine: dorsal view, X 9.

21, 25, 27. Paratype pygidium: 21, oblique posterior view showing tips of major border spines and openings at base of barbs, X 30; 25, posterior view, X 6; 27, dorsal stereograph, X 6. Locality 2, USNM 124712d.

22, 23. Incomplete segment from posterior part of thorax: dorsal and left lateral views, X 6. Locality 2.

24. Tip of major border spine of pygidium showing openings at base of barbs, X 30. Locality 2.

26. Paratype, 2 incomplete segments from posterior part of thorax: dorsal view, X 9. Locality 3. USNM 124712c.

28. Pygidium: dorsal stereograph, X 6. Locality 2.

Bulletin of the Museum of Comparative Zoology

AT HARVARD COLLEGE

Vol. 114, No. 6

A CAT SKELETON WITH AN ANOMALOUS THIRD HIND LEG AND ABNORMAL VERTEBRAE

By

Thomas S. Parsons

and

John M. Stein

With Four Plates

CAMBRIDGE, MASS., U.S.A.

PRINTED FOR THE MUSEUM

May, 1956

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May, 1956

No. 6 — *A Cat Skeleton with an Anomalous Third Hind Leg and Abnormal Vertebrae*

By Thomas S. Parsons and John M. Stein

Harvard Biological Laboratories
Cambridge 38, Massachusetts

INTRODUCTION

The cat skeleton here described (see Plate 1) displays on the right side a highly abnormal innominate bone articulating with two legs, the more anterior of which has two tibiae and is evidently the product of a fusion of two legs. The posterior vertebrae show various fusions and abnormalities. The skeleton was kindly lent to us by its owner, Mr. Elling O. Eide, of Sarasota, Florida. The cat was a family pet which lived over six and a half years and could run and climb trees despite its extreme pelvic abnormalities. Its appearance in life is shown in Plate 3A. It was buried shortly after its death and the skeleton dug up fifteen months later. Although a few of the smaller bones were not recovered, the completeness of the recovery is shown by the finding of twenty-eight of the sesamoids.

The mother of the cat was apparently normal and produced many litters of kittens, probably many by the same father whose only abnormality was polydactyly. The one described here had two normal littermates. The mother was slightly over seven and a half years old when this litter was born. She was very sick for several weeks after their birth, but recovered and had normal litters afterwards. Most of her kittens were normal except for numerous cases of polydactyly, but one born approximately three years before the one here described had two symmetrically fused heads. It was found dead, and whether or not it was alive at birth is not known.

Due to the burial, only the skeleton of the animal was recovered, and no attempt has been made to reconstruct any of the soft parts. The skeleton has, however, been compared with five normal ones, one articulated and four disarticulated, as well as with the extensive descriptions and illustrations in Jayne (1898).

The only definite evidence on the articulation of this skeleton in life comes from the nature of the articulatory surfaces and the excellent x-ray shown in Plate 2. The skeleton was mounted as shown in Plate 1; no attempt was made to include most of

the tail, the ribs, sternum, phalanges, or hyoid apparatus in this reconstruction.

Although the work of making the original descriptions was divided between the authors, both of us have gone over all the parts and are equally responsible for this account. In order to give morphological descriptions, it is necessary for us to give names to several of the anomalous elements before the reasons for our interpretations of their nature can be stated. However, we hope that the reader can separate our theories from the more objective accounts of the various bones.

We would like to thank several people for their kind assistance in the writing of this paper: first, Mr. Elling O. Eide, who not only loaned us the skeleton, but also gave us its history, provided the photograph of the live cat, and made the drawings; Dr. C. K. Newton, D.V.M., of Bradenton, Florida, who provided the x-ray of the hind legs; and especially Dr. Ernest E. Williams of Harvard University, who offered much helpful advice throughout the course of the study.

DESCRIPTION

General

Much of the skeleton, such as the pectoral girdles and limbs, is normal and needs no detailed description. The skull and jaws are also normal, but have a very stocky appearance. Both are short and very wide; the areas of attachment of the jaw muscles are noticeably larger than average. The canine teeth are very large. The third right lower premolar, the third right upper incisor, and the third left upper premolar are missing and the sockets filled with bone, but these probably were lost after maturity was reached. The two second upper premolars are also missing, but they seem never to have been present, a relatively common occurrence, according to Jayne (1898). The first and second left upper incisors were broken off, apparently before death. Only the two stylohyals of the hyoid apparatus were recovered. They appear normal.

The ribs seem normal except that the twelfth right one is lacking due to the malformation of the vertebra. The recovery of the sternum was incomplete, but the manubrium and five sternebrae (two of them fused) are present. All appear slightly thicker

than usual for their length, especially the fused pair. Their ends appear rather asymmetrical, but in the absence of the cartilages between them this indicates little. The fused ones each send out a short prong of bone, on either side, at the fused ends which must have articulated with the costal cartilages.

Vertebral column

The anterior half of the vertebral column appears normal; the posterior part shows abnormalities. There are seven cervicals, thirteen thoracics, seven lumbars, four sacrals (one more than usual), and nineteen caudals. The last number, although low, is within the range given by Jayne (1898), and some of the terminal ones may not have been recovered. Only those vertebrae which show marked peculiarities will be described here.

The first such is the tenth thoracic. The neural spine and postzygapophyses are twisted approximately 15 degrees to the left. The posterior articular surfaces are more nearly horizontal and the anapophyses shorter than usual, but this vertebra is still relatively normal in general appearance.

The last three thoracic vertebrae are fused into one mass (Fig. 1). The eleventh is joined to the twelfth by the dorsal part of

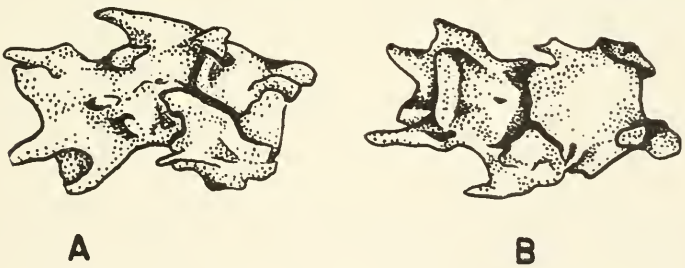

Fig. 1. Eleventh, twelfth, and thirteenth thoracic vertebrae. Anterior end to right. A, dorsal view. B, ventral view. x1.

the centrum and a small flange of bone just ventral to the left anapophysis. In the former the two sides of the neural arch meet dorsally in the midline, but are not fused, and there is no trace of a neural spine. All of the articular processes appear quite normal in shape, although the postzygapophyses are deflected slightly to the left and the right metapophysis is more anterior

than lateral to the prezygapophyseal facet. Well developed tubercular facets are present and the capitula of the ribs articulate intervertebrally as is usual in the more anterior thoracic vertebrae, but not common in the eleventh (see Jayne, 1898, p. 84; however, his fig. 55, p. 82, shows a situation similar to that in this specimen).

The twelfth thoracic vertebra is represented ventrally only by the wedge-shaped left half of the centrum (Fig. 1B). On the right side the eleventh and thirteenth thoracics come together without any gap between them. Dorsally (Fig. 1A), both sides of the neural arch of the twelfth are present and tightly fused to the last thoracic, but the right side is far smaller than the left. Only a left rib articulates with this vertebra, and that to a large convex capitular facet. The prezygapophyses are quite normal, but the right metapophysis is much reduced. The postzygapophyses are fused with the prezygapophyses of the following vertebra forming dorsal mounds. An anapophysis is present only on the left. The small neural spine points straight dorsally. This vertebra is thus anticlinal, using Jayne's (1898) definition; he gives the eleventh as the normal anticlinal vertebra, while Gottlieb (1914) states that it can be either the tenth or the eleventh. The intervertebral notch on the right appears double, so presumably the normal number of spinal nerves was present.

The thirteenth thoracic vertebra (Fig. 1) is the most normal looking of the three fused ones. The prezygapophyses lack distinct metapophyses due to their fusion with the postzygapophyses of the preceding vertebra, but there are raised roughened areas which probably correspond to them. The neural spine is quite small and directed anteriorly. The postzygapophyses and anapophyses are displaced to the left with the right ones dorsal to the left. The latter are normal, but the right postzygapophysis is elongate, while the right anapophysis is higher than long, articulating with the entire height of the following prezygapophysis.

The first lumbar vertebra (Fig. 2A) is markedly asymmetrical with its centrum about 9 mm. long on the right side and 12 mm. on the left. The neural arch appears slanted to the left so that the left pedicle is abnormally thick while the right, although in contact with the centrum, is not fused to it. The neural canal is thus displaced to the right. The right prezygapophysis is vertical

and massive while the left is thinner and projects dorsolaterally. Only the latter bears a normal metapophysis. The postzygapophyses are both displaced to the left as are the anapophyses. The

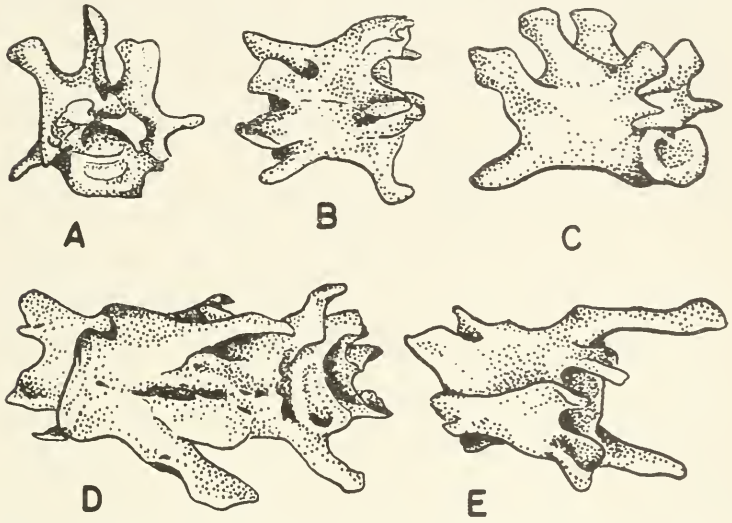

FIG. 2. Lumbar vertebrae. Anterior end to right in B, D, and E and to left in C. A, first in posterior view. B, second in dorsal view. C, third in posterolateral view. D, fourth and fifth in ventral view. E, sixth in dorsal view. x1.

latter are quite short and round in section with the right one well dorsal to the left. The rather small neural spine arises from the normal position on the neural arch and slopes towards the right to the midline. The pleurapophyses are rudimentary prongs about 2 mm. long on the right, and 4 mm. on the left. The former is somewhat dorsal to its usual position while the latter is curved slightly posteriorly.

The second lumbar vertebra (Fig. 2B) is also highly asymmetrical. The prezygapophyses, massive structures with nearly vertical articular facets, are displaced to the left with only the right bearing a normal metapophysis. The postzygapophyses and anapophyses appear quite normal, the only irregularity being a slight elongation of the right postzygapophysis. As in the first lumbar, the neural spine leans to the right, almost meeting the

right prezygapophysis. The pleurapophyses are very small and do not extend ventral to the centrum. The right one points laterally and the left anteriorly.

The third lumbar vertebra (Fig. 2C) displays spina bifida with both sides of the neural arch forming a separate neural spine. The middorsal cleft is exceedingly narrow, but the two sides do not actually touch at any point. The left neural spine is directed anteriorly and appears much like the anterior half of a normal neural spine. The more posterior right one is directed straight dorsally so that a V-shaped notch is seen between them in lateral view. All the zygapophyses and metapophyses are normal with the left prezygapophysis and right postzygapophysis slightly larger than the others. The anapophyses, especially the left, are reduced in size and are spinous rather than blade-like. The pleurapophyses while normal in shape are also reduced, being intermediate in size between those of the first and second lumbar vertebrae of the four normal cats used for comparison.

The fourth and fifth lumbars (Fig. 2D) are fused by a large rounded mass of bone ventral to the two centra. The normal parts of the two, which are held in the articulated position, show no fusion. The ventral mass is fused to the sides of the centrum of the fourth lumbar leaving a small midventral canal between it and the centrum; no such canal is present in the following vertebra. The anterior face of the fourth lumbar centrum faces anteroventrally producing a distinct angle in the articulated spine at this joint. The pleurapophyses are small and more ventrally directed than usual. The right one points slightly more laterally than the left. The metapophyses are not distinctly developed and the left anapophysis is rudimentary; otherwise the processes of this vertebra are normal.

The fifth lumbar vertebra also has quite normal dorsal processes. The right anapophysis is almost completely absent, a condition which was also seen in the normal skeletons used for comparison. The left postzygapophysis is slightly elongated, and the posterior end of the neural spine is deflected to the right. The other processes show no modifications. The pleurapophyses are somewhat reduced (Fig. 2D), and the right one especially does not extend laterally as far as usual. The complex of the fourth and fifth lumbars shows a slight curvature with the length of the two centra slightly greater on the left than on the right. It

is impossible to say exactly how this curvature is brought about because of the mass of bone ventral to the two centra obscuring their articulation.

The sixth lumbar vertebra (Fig. 2E) also has greatly reduced pleurapophyses with the right one considerably smaller than the left. Both extend anteroventrally but not laterally, as would be the normal condition. The posterior face of the centrum is somewhat dorsally directed, thus making another sharp angle in the articulated spine. The prezygapophyses and metapophyses are normal with those on the left slightly larger. The neural spine leans towards the left. On the right, the postzygapophysis is much reduced and the anapophysis completely absent, while on the left the former is greatly enlarged and the latter present although very small.

The seventh lumbar vertebra is tightly fused to the sacrum dorsally, although ventrally the centra remain separate (Fig. 3). It does not enter into the sacroiliac joint. The left pleurapophysis, while short, is fairly normal, but the right one is absent except for a broad truncated base extending just anterior to the side of the centrum. The left prezygapophysis is a simple dorsal projection lacking a metapophysis completely (as in one of the four disarticulated normal cats used for comparison). On the right the entire process is a low mound reaching posteriorly as far as the right neural spine. The left postzygapophysis is completely fused to the prezygapophysis of the first sacral vertebra, the two being represented by a small mound. There is no trace of any corresponding articulation on the right. The neural arch apparently did not fuse middorsally until very late in development since there is a distinct suture curving to the left posteriorly. Two neural spines are present, their arrangement being similar to that in the third lumbar except that in the seventh the right is anterior. The latter expands anteroventrally where it has a concave anterior face into which the prezygapophysis extends. The neural canal is triangular rather than quadrilateral in end view.

The sacrum is shown in Figure 3. It is, as a unit, somewhat twisted. The posterior part is slightly curved to the left, mainly by unequal growth of the sides of the second sacral vertebra, and accompanying this there is a counterclockwise rotation about the long axis of the body when seen in posterior view. The left side

of the sacrum is quite normal despite the presence of a fourth sacral vertebra. There are three small mounds representing fused zygapophyses and three sacral foramina both dorsally and ventrally. The sacroiliac joint on this side is apparently normal

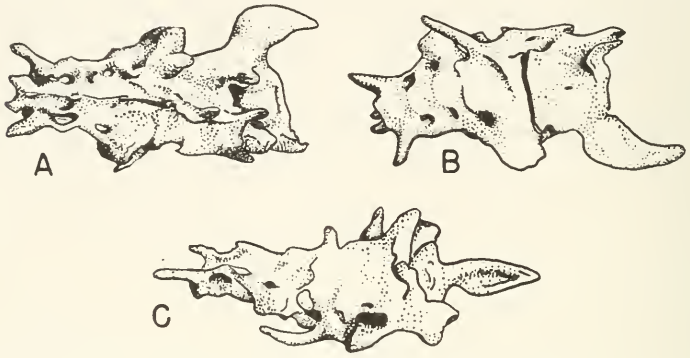

FIG. 3. Seventh lumbar vertebra and sacrum. Anterior end to right. A, dorsal view. B, ventral view. C, lateral view. x⅔.

although the auricular facet is slightly larger than figured by Jayne (1898, fig. 75, p. 103) or in the four normal cats examined. The neural spines are fused into a low longitudinal ridge with a definite spine for the first, and small gentle rises for the middle two, but no distinct spine on the fourth sacral. The left pleurapophysis of the fourth sacral is slightly smaller and more laterally directed than the right.

The right side of the sacrum is highly abnormal. There are no signs of the three pairs of fused zygapophyses and only the posterior two pairs of sacral foramina are normal. The surface articulating with the ilium is split into two separate parts. The larger and more posterior is an irregular, posterolaterally directed, oval facet on the expanded transverse process of the second sacral. The other is a small circular facet at the posterior end of the first sacral about midway dorsal. It is laterally directed. The first sacral lacks a large expanded transverse process on the right, having only this articular facet on a small process which does not extend as far laterally as the second sacral (from which it is separated by a narrow groove), and a posteriorly directed ventral process somewhat resembling a caudal rib. This

ends just ventral to, but not fused with, the transverse process of the second sacral. There is thus neither a dorsal nor a ventral sacral foramen between these two vertebrae, but a large lateral intervertebral foramen.

Of the nineteen caudals, only the first six show any abnormalities. The first three show slight asymmetries in the zygapophyses, but nothing else unusual. Numbers four through six are fused together by their neural arches, with their centra remaining quite distinct. As in the last three thoracics, the middle one, the fifth caudal, is represented only by one side, in this case the right. Apparently the left side is completely absent even dorsally, the postzygapophysis of the fourth articulating directly with the prezygapophysis of the sixth on that side. On the sixth there is a small prong of bone on the centrum representing part of a haemal arch; a similar condition was observed in one of the normal cats used for comparison.

Pelvic girdles and appendages

The left innominate bone seems quite normal except that the auricular articulation is unusually large and the spine of the pubis for the attachment of the rectus abdominis is absent. One of the normal cats used for comparison also lacked the latter structure. The left femur, tibia, and fibula all appear quite normal.

The right innominate bone (Fig. 4) is a very deformed structure, seemingly divided into two parts: one part consists of the right half of the more normal or left pelvis; the other is a very disfigured complete second pelvis. This second or teratological pelvis and the more normal right innominate are solidly fused in two places: one between the spine and horizontal ramus of the more normal pubis and the medial portions of the teratological right ischium, the other between the anteromedial portion of the more normal ilium and the anterolateral portion of the teratological right ilium. A distinct opening occurs between the two points of fusion (Fig. 4A, *oi*). Thus the teratological pelvis is suspended by the more normal right innominate in a parasagittal plane of the animal. The part of the teratological pelvis normally ventral faces laterally to the right.

The ilium of the more normal right innominate is about 1 cm.

shorter than the left. The suture (Figs. 4A and B, *sut*) between the two ilia is solid yet clearly defined. Approximately 7 mm. posterior to the suture on the medial side is an oval articulation with the sacrum (4x7 mm. in size; Fig. 4A, *a1*).

Starting about 10 mm. from the anterior end of the ilium and extending for 40 mm. on the lateral side and even overlapping for

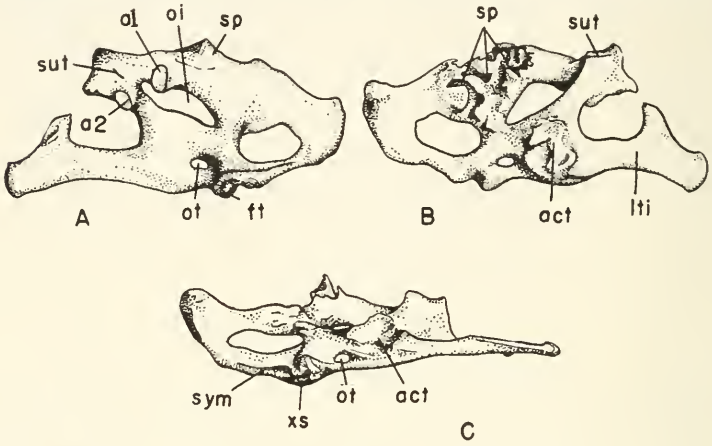

Fig. 4. More normal right innominate and entire teratological pelvis. A, medial view. B, lateral view. C, ventromedial view. Abbreviations: *a1*, regular auricular facet; *a2*, right auricular facet of teratological pelvis; *act*, acetabulum of teratological pelvis; *ft*, ischial tuberosities of teratological pelvis; *lti*, left teratological ilium; *oi*, gap between regular right innominate and teratological pelvis; *ot*, obturator fenestrae of teratological pelvis; *sp*, spongy bone mass; *sut*, suture between regular right innominate and teratological pelvis; *sym*, regular pubic symphysis; *xs*, bony ridge ventral to pubic symphysis. x1½.

12 mm. on the medial surface lies a spongy mass of bone (Figs. 4A and B, *sp*). Part of this spongy mass forms the articulation for the more normal right femur. The acetabulum is irregular in shape and has a very rough surface as does the head of the articulating femur. This spongy bone seems to have replaced arthritic cartilage and to have been applied to the more normal bone underlying it. Some rough bone also appears on the medial side of the ischium, dorsal to the obturator fenestra.

The ischium of the more normal innominate is bent ventrally and laterally to the right more strongly than in any of the four cats used for comparison. The bone on the ventral side of the ischium is rough and the tuberosity is unusually large. At the symphysis, the fit between the right and left halves of the left pelvis is good, but a small ridge of bone extends ventrally along the entire right part of the symphysis (Fig. 4C, *xs*). The descending ramus of the pubis of its right innominate is much thicker dorsoventrally than that of the four normal specimens. The horizontal ramus is fused with the teratological right ischium for about 17 mm. This suture is very solid, but the line of fusion can be seen quite clearly by the grain of the bone.

The teratological pelvis looks like a fat, symmetrical "Y" from a lateral view. There is a small fenestra near the base of the Y, this presumably being the fused obturator fenestrae from both sides (Fig. 4A, *ot*). The right ilium (the posterodorsal arm of the Y) is shorter than the left and has an oval auricular facet (Fig. 4A, *a2*) about 3x5 mm., located 9 mm. from the right upper end of the Y, and 4 mm. from the line of fusion with the more normal right ilium. The teratological left ilium is located on the right side of the cat's central axis. The left teratological ilium looks slightly more normal in shape than the right teratological one does. The right pleurapophysis of the seventh lumbar vertebra is fused to the left teratological ilium. It will be remembered that the rest of the seventh lumbar is fused to the sacrum.

From ventrolateral aspect, the teratological innominate has one fairly smooth acetabular articulation (Fig. 4B, *act*). This articulation has two distinct sides, right and left. Posterior to the fused obturator fenestrae are the fused tuberosities of the ischia (Fig. 4A, *ft*). The ilia on both sides are of smooth solid bone.

The articulation of the femur with the more normal right innominate is a knotty, gnarled mass of bone (Fig. 5A, *ar*). The articular surface itself seems worn enough to have allowed some slight movements. The abnormal area seems to have been formed on top of smoother bone and is probably ossified cartilage. Only the posterolateral part of the head is present and that is formed in rough bone. An irregular pit occurs in place of the rest of the head (Fig. 5A, *pt*). The lesser trochanter (Fig. 5B, *lt*), also covered with rough bone, seems also to have articulated with the innominate slightly posterior and medial to the head articu-

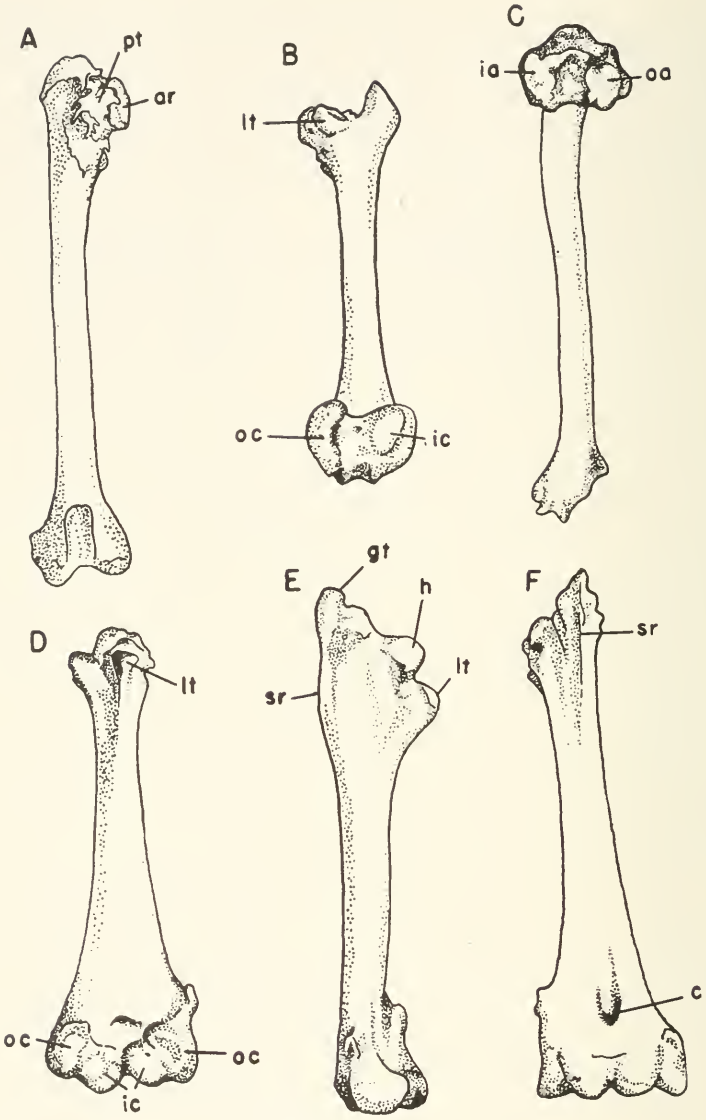

Figure 5

lation. This places the femur in a position approximately perpendicular to the central axis of the cat. The shaft is almost cylindrical, i.e., not graded in thickness as were those of the cats used for comparison. Although slightly rough in appearance, the greater trochanter has a normal shape. Distally, the condyles are bent about 15 degrees medially, considering the bone in the normal position (Fig. 5B). The articulatory surfaces of the condyles are smaller than those of the four normal cats; they are also slanted inward towards the axis of the bone and do not extend outward as they should. The medial condyle has a long curved articulation (Fig. 5B, *ic*); the lateral condyle has a short oval articular surface (Fig. 5B, *oc*).

Proximally the more normal right tibia has unevenly developed articular surfaces. The lateral articular surface (Fig. 5C, *oa*) is less extended than in the normal cats, whereas the medial surface (Fig. 5C, *ia*) extends in an arc with the lateral articulation as a center. Considering the shape of this articulation and that of the distal end of the femur, it seems as though the knee joint had a swivel action as well as a hinge in order to compensate for the very slight motility of the acetabular articulation. The rest of the bone appears normal, as does the fibula of this leg.

The fusion of two femora, one right and one left, apparently formed the double femur which articulates at *act*, Figure 4B, with the fused teratological pelvis. The articulation is smooth and allowed hip movement. The distal portions of the femora are fused at an angle of about 60 degrees (Fig. 5D). Proximally the two component bones have turned so that their heads and the greater and lesser trochanters all have fused with their counterparts from the other side, the double bone having one head, one greater trochanter, and one lesser trochanter all located in the

FIG. 5. A and B, more normal right femur in anterior and posteroventral views. C, more normal right tibia in posterodorsal view. D, E, and F, fused teratological femur in actual ventromedial (morphological posterior), actual anterior (morphological left lateral), and actual lateral (morphological anterior) views, respectively. Abbreviations: *ar*, irregularly formed head; *c*, canal; *gt*, greater trochanter; *h*, head; *ia*, medial tibial condyle; *ic*, medial femoral condyle; *lt*, lesser trochanter; *oa*, lateral tibial condyle; *oc*, lateral femoral condyle; *pt*, rough pit; *sr*, sharp ridge. B, C, and D foreshortened to show articular surfaces. x⅔.

medial plane of the bone (Fig. 5F). On one side at the proximal end in the medial plane there is a sharp thin ridge (Fig. 5F, *sr*) running for about 25 mm. In this region the bone is thin lateromedially and thick anteroposteriorly. Moving distally, the bone gradually widens lateromedially and at the distal end is as thick that way as it was anteroposteriorly before (Figs. 5E and F). A canal (Fig. 5F, *c*) perforates the bone starting anteriorly (here and for the rest of the description of the long bones of this leg, anterior, posterior, medial, and lateral refer to the normal position, not that in this specimen) about 25 mm. from the distal extremity and ending 10 mm. from that end on the posterior side. This canal is directly in the midline of the bone. A large articulation for a sesamoid is present on the lateral surface of the right component. All four condyles are well formed (Fig. 5D). The x-ray shown in Plate 2 gives the relationships at this joint clearly.

The two separate tibiae which articulate with the double femur are almost exact mirror images of each other. They lie so that their anterior surfaces are pointed outward from their mutual articulations. These articulations between the two tibiae lie one at the posterior side of the head (Plate 2) and the other at the distal extremity. There are two proximal articular surfaces on each of the bones; they lie on the posterolateral and anteromedial parts of the head. It appears that the joint between the double femur and the two tibiae must have been almost completely immobile. The shafts are unusually thin and the bones are disproportionately long in comparison to the other bones in the cat. The tubercle is prominent and the crest is short. Distally all the parts are recognizable, although modified.

The overall organization of this double leg is rather baffling to the authors. The anterior halves of the teratological pelvis and of the double femur appear to represent the morphological left side, an interpretation which fits not only the shape of the elements, but also the most probable pattern of fusion. Nonetheless, certainly in the foot and very probably in the lower leg, the morphological left is posterior. It is as though the knee were mistakenly articulated backwards in the mounting of the skeleton; however, the nature of the articular surfaces and the photographs of the living cat seem to preclude this latter possibility.

The double fibula is a symmetrical structure formed by the

complete fusion of two fibulae, one right and one left, along their medial sides. At the proximal end, the fusion has caused the loss of the medial parts of both bones, leaving only the lateral parts recognizable. The shaft is thin and bent concavely from the posterior aspect. Distally the median parts of the bones are not lost. There is a fossa with a central ridge in the line of fusion and indications of the lateral maleoli are present on both sides. The astragalar articulations form one single articular surface which is quite rough.

The feet of both the regular hind legs appear completely normal, but the tarsus of the abnormal limb is much modified by being in the flexed rather than the normal extended position so as to form an angle of about 120 degrees with the tibiae. This tarsus is a double structure bearing metatarsals 1, 2, 3, 4, 3, 2, and 1, hence with two sides corresponding to the normal median and without any normal lateral. In the description, dorsal, ventral, lateral, and median will be used for the condition in this foot; all are the reverse of the normal morphological pattern. Although only the disarticulated bones are available, the articular surfaces can be matched very precisely in all cases so that the restoration is almost certainly correct although two elements are missing (Plates 3B, C, and 4).

The calcanea, astragali, and scaphoids are fused into one symmetrical mass, but in most places the sutures can be distinguished. The first form a single midventral bar which expands posteriorly in a rough and immovable articulation with the single fibula and both tibiae. Each astragalus is an L-shaped element with the two arms of approximately equal length. It lies along the side of the calcaneum and has one arm extending dorsally from its proximal end to form the main articulation with the tibiae. The dorsal surfaces are fused into one triangular facet with the apex anterior. The scaphoids are fused together and cover the distal ends of the astragali, but not the more ventral calcanea. The tuberosities are thus dorsal and lateral.

The cuboids are represented by a single midventral element which articulates proximally with the calcanea and dorsally with the scaphoids and ectocuneiforms. It is more or less cylindrical with the length about twice the diameter. The distal end is concave to receive the proximal end of the single fourth metatarsal.

On the left, the ectocuneiform and mesocuneiform are fused

into a single element which covers almost all of the distal surface of the left scaphoid. The part representing the mesocuneiform is far larger than usual being almost equal to the ectocuneiform in size. However, the former is, as usual, shorter in the proximal-distal direction. The articular surfaces have the same general pattern as in normal specimens, but those of the mesocuneiform are much expanded, especially in height. The left entocuneiform and probably also the vestigial first metatarsal are represented by a single fairly normal-appearing element which lies in the expected position dorsal and lateral to the mesocuneiform and proximal end of the second metatarsal. It also articulates with the scaphoid.

On the right, only the ectocuneiform is present. It is, like most of the elements of this tarsus, smaller than usual, compared to normal cats of the same overall size. It lies distal to the ventromedian half of the right scaphoid. The hook on the plantar (here dorsal) surface is much reduced and the ventrolateral corner is drawn out into a small prong, but the element is immediately recognizable as an ectocuneiform. The mesocuneiform was lost but, judging from the articular surfaces of the scaphoid and second metatarsal, must have been quite large and similar to the one on the left. The right entocuneiform and first metatarsal are also lost and were probably similar to the left, although there is no smooth articular surface for them on the right scaphoid. It is possible that these elements were never present. The overall symmetry of the foot and the notch on the dorsolateral surface of the proximal end of the second metatarsal strongly suggest their presence however.

The five metatarsals require little description except for the middle one (number 4, probably representing a fusion of that element from both sides). The others, numbers 2 and 3 of each side, bear normal proximal articular surfaces although those of the third metatarsals are in contact with each other dorsally and both have a small facet for this articulation. The distal ends of these third metatarsals are normal while the seconds both end in rather amorphous rounded swellings. These four are all curved with the concave surface dorsal; that is, they are not modified for the inverted position of the foot. The outer pair are also curved laterally at their distal ends. The right second metatarsal is somewhat shortened, but the other three are all normal length

although considerably thinner than is usual.

The central, fourth, metatarsal is a symmetrical element with both ends much modified. Proximally, it bears a small convex head articulating with the cuboid, while distally it has a larger convex swelling with a small dorsal projection. The curvature is the reverse of the other metatarsals with the concave surface ventral. It lies ventral as well as median to the third metatarsals and is in contact with them proximally. This gives it a triangular shape in section although it is rounded distally. Its length is equal to that of the third metatarsals.

There are also three phalanges presumably associated with this foot. However, their position cannot be told from the disarticulated bones and it is possible that some were lost. Two of the three have fairly normal proximal concave faces, and distally small swellings showing none of the usual features. The third is a short thin cylindrical bone without any distinctive features.

DISCUSSION

General

The main significance of highly abnormal specimens is the information they may give concerning developmental processes or inheritance; however, detailed consideration of these points is not possible in this case although we will mention possible genetic mechanisms. It is hoped that the description is detailed and accurate enough to give future workers another example which will be useful in reaching any general conclusions.

The literature of teratology and the genetics of abnormal development is very extensive and no attempt at compiling a complete bibliography of the described abnormalities was made. The papers cited include only those available ones which seem to bear most directly on the problems discussed. More extensive bibliographies of teratology can be found in such general works as Bateson (1894), Schwalbe (1906-1913), Schlegel (1921), and Ströer (1937). Grüneberg (1947) includes many references to the genetical literature, especially concerning rodents.

Vertebral column

The anomalies shown by the vertebrae of this cat are all well known and have been much studied, especially in humans. However, single specimens with so many deformities are rare and seldom reach maturity. While some of the peculiarities may be a direct result of the pelvic malformation, others, though quite possibly caused by the same factors, are not. Possibly some, such as the fusion of the fourth and fifth lumbars, were caused by disease after maturity was reached and are thus outside the province of this discussion.

Spina bifida (or rachischisis) is a well known defect, but in most studies on teratology only extreme cases are considered (as in Kermauner, 1909). Examples such as the eleventh thoracic and third lumbar of the present specimen should have little or no adverse effect upon the animal and hence are of small interest medically. Probably such cases are of more frequent occurrence than the literature would indicate since Jayne (1898) apparently found at least one in the cats he used (see his fig. 83, p. 125). Unfortunately he does not say how many were examined, but he had at least part of fifty or more spinal columns. In mice there are many mutations which can cause spina bifida (Grüneberg, 1952).

The two half-vertebrae, the twelfth thoracic and fifth caudal, also represent a well known anomaly of great theoretical interest. Baur (1891), on the basis of several reptilian skeletons, put forth a theory of increase in the number of segments by intercalation with such hemivertebrae representing incomplete cases. Brash (1915) studied a human spine with this defect in a cervical, and reviewed the literature on all cases reported in man. He concluded that the hemivertebrae could arise from either the addition or loss of half of a normal vertebra and that in his specimen the condition was secondary, with the absence of the spinal nerve on one side as the primary cause. Similar cases have been reported in many forms including the cat (Jayne, 1898, fig. 84, p. 125). The twelfth thoracic in our specimen is presumably an example of the failure of half of the centrum to form, since counting it there are the usual thirteen thoracics. Judging from the foramina, the normal number of spinal nerves was present, so here the condition is primary. Concerning the fifth caudal, no

definite statements can be made.

Even commoner and better known are variations in the number of sacral vertebrae. Bateson (1894) gives many cases of this and Dwight (1901) discusses its occurrence in man. Jayne (1898) mentions its occurrence in the cat. The incorporation of the first caudal into the sacrum is not very common according to the last author, but no figures are given. On the other hand, partial fusion of the seventh lumbar and sacrum, often with a tendency for the lumbar to become involved in the sacroiliac joint, is exceedingly common. Klatt figures such a condition in a dog and a cat (1939, figs. 7 and 8, pp. 230 and 231). In the present case there is no actual participation of the last lumbar in the joint, but the right side shows modifications of the pleurapophysis. This seems to approach sacral articulation with the extra pelvis.

More recent workers such as Danforth (1930b) and Backman (1934) consider the boundaries between the various regions of the vertebrae to be determined by gradients in differentiation. Thus the homology of individual vertebrae cannot be determined by simple counting, whether from the anterior end or any other selected point. This opinion seems well confirmed by the work of Sawin and his co-workers, especially Green, on the lumbar region in rabbits and mice (see Grüneberg, 1947, for references). The twenty-seventh vertebra in the cat here described is, according to this conception, partly sacral as well as lumbar; the name seventh lumbar is used merely as a convention. This viewpoint also casts grave doubts on the earlier ideas concerning hemivertebrae mentioned above.

The spinae bifidae and hemivertebrae could be independent of the leg anomalies with the sacral malformations directly dependent on the latter, although similar cases of deformed sacra are known where there are no pelvic abnormalities. However it is also possible that all the spinal abnormalities are a result of the pelvic duplication since they are all consecutive, running from the tenth thoracic through the sixth caudal. The general asymmetry of the posterior part of the vertebral column may also be partly or wholly dependent on the other anomalies since certainly the muscles must have been very abnormal in this area. However such asymmetry is well known especially in the tail where it is very common in some forms such as certain dogs which

are otherwise quite normal (see Klatt, 1939, and Stockard et al., 1941, for a discussion of this). Berg (1912) describes a series of cats in which the tail is greatly deformed. However, in almost all these cases the tail is markedly shortened and the malformation usually is greatest distally, neither of which is true of the cat under consideration. The genetics of such deformed tails has been studied by a large series of workers, but is not well understood and need not be considered here. Bamber (1927) reviews the genetical literature on cats.

In mice and other rodents there are many mutants listed by Grüneberg (1947 and 1952) which show similar deformation of the caudal vertebrae. The morphological expression and genetic action of these various mutations are very diverse. While most of them tend to shorten the tail, some such as the mutation 'flexed' (Hunt, Mixter, and Permar, 1933) have no such effect. In rats, 'stubs' (Ratcliffe and King, 1941) affects not only the tail but also causes abnormalities in the hind limbs. Both of these are recessive genes. There are also several dominants such as 'Brachyury' or 'T' (Chesley, 1935) and 'Sd' (Gluecksohn-Schoenheimer, 1943) which are lethal when homozygous. It is of interest that in a mouse of genotype T/+ Sd/+ there is a cumulative effect producing a more highly aberrant vertebral column than either gene does alone, although both normally produce a similar effect (Gluecksohn-Schoenheimer, 1943). Most of these mutations cause not only asymmetry of the vertebrae, but various other defects, such as spina bifida, are common in mice bearing these mutant genes.

It therefore seems possible, though in no wise proven, that the vertebral column of this cat developed abnormally under the control of a mutation similar to some of those known for mice, and that this abnormality was accentuated by the occurrence of another developmental anomaly, genetically controlled or not, resulting in the formation of a second and much modified pelvis and pair of limbs. Another possibility is that all the anomalies are the result of a single event, either a mutated gene or some environmental factor operating during the very early development. If it is a single mutation, then it would probably be dominant although there is the possibility of a recessive or the extreme expression of a homozygote in which the heterozygote is relatively normal as in Wright's (1935) polydactylous guinea

pigs. Any such theory postulating homozygosity for a mutation in this cat would almost certainly require that the father was not the one suspected but a half-brother of the cat being studied, since the chance of the same mutation appearing in two unrelated cats is very small. Another problem which arises in considering possible genetic mechanisms is that any genes involved may show a very low penetrance, as is the case in Danforth's (1925 and 1930a) strain of mice to be discussed below. Thus, for example, the mother and approximately half her offspring could be carrying a gene responsible for the abnormalities described in this specimen without their showing any phenotypic effects.

Pelvic girdles and appendages

Like most described polymelous specimens, this cat exhibits posterior duplication — however, in a much modified form. The commonest pattern of such abnormalities appears to be one in which two approximately equal pelvic girdles are present, producing a Y-shaped main axis of the animal. However, the spinal column is usually single and much deformed posteriorly. In such cases there is a marked tendency for the reduction and fusion of the inner pelvic elements of the two sides. Cases in point have been described by Conrow (1917) and Mainland (1929) where six legs were clearly present, and by Lesbre (1900) and Horsley (1920) where fusion has reduced the number to five.

Reports of cases of asymmetry like the present one are somewhat rarer and far less complete. Murie (1934) reports a five-legged rabbit, but very little is told of the nature of the extra leg. Three other papers describe animals in which the doubling is confined to the appendicular skeleton on one side with the other side essentially normal: Bateson's (1894) macaque (his no. 504) shows this doubling extending into the pelvic girdle while in Weimer's (1942) sheep only the limb, and in Dwight's (1892) human, only the forearm and hand are affected.

The cat under consideration conforms to neither of these patterns. There is posterior duplication resulting in four pelvic limbs and two girdles. Reduction and fusion characterize the right girdle (the teratological pelvis of the descriptive part) and limbs, while the left side remains essentially normal except for the right innominate, thus forming the more normal pelvic girdle of the cat. It is impossible to tell whether any duplication oc-

curred in the soft parts. However, the viscera probably did not show much duplication since the right pelvic canal is completely closed by extensive fusion.

As mentioned previously, fusion in the limb is a common feature of polymelous specimens, there being great variation in degree. Here the femora, fibulae, and feet are very closely fused but the two tibiae are completely separate. The macaque of Bateson (1894) is very similar in this respect except that there the positions are reversed and the fibulae are separate and the tibiae joined together.

There is very little known about possible genetic mechanisms causing such posterior duplication. Danforth (1925 and 1930a) has described a mutant strain of mice with this character, but the exact mode of inheritance is not known. By selecting for it, he was able to develop only a line with an incidence of 12 per cent, so it is considered probably recessive. The expression was very variable with extensive fusion normally occurring. The spinal column was also abnormal with the tail generally kinky, and occasional cases of spina bifida. In the case of the cat described in this paper, there is no evidence that the cause of the duplication is genetic as opposed to environmental.

The functional problems arising from the extra leg are of some interest, but little can be definitely said about them. It seems most unlikely that the much deformed double foot could have borne any weight, so that leg was presumably of little use despite the very smooth hip articulation. The more normal right leg, on the other hand, has much irregular and apparently arthritic ossification at the hip resulting in what must have been an almost immovable joint. Despite the presumably compensatory freedom at the knee evidenced by the articular surfaces there, this leg too would seem greatly inferior to the normal condition. Thus it seems probable that the cat depended on the three normal limbs, making little use of the two right hind legs.

SUMMARY

The cat skeleton described in this paper shows an unusual type of posterior duplication in which the left pelvic girdle and limbs are relatively normal and the right ones much modified. The right girdle is a single Y-shaped element fused to the anteroventral border of the right innominate of the left pelvis, and bears

one limb. This consists of a single element representing two femora, two tibiae, one fibula, and a highly abnormal foot in the flexed position bearing metatarsals 1, 2, 3, 4, 3, 2, and 1. The vertebrae from the tenth thoracic through the sixth caudal are all abnormal showing various degrees of asymmetry and fusion and cases of spinae bifidae and hemivertebrae. Possible genetic causes of such a condition are discussed, but no definite conclusions can be reached concerning this case.

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PLATE 1

PLATE 1. Mounted skeleton of the cat. The greater part of the tail, the ribs, sternum, phalanges, clavicles, patellae, and hyoid apparatus are not included.

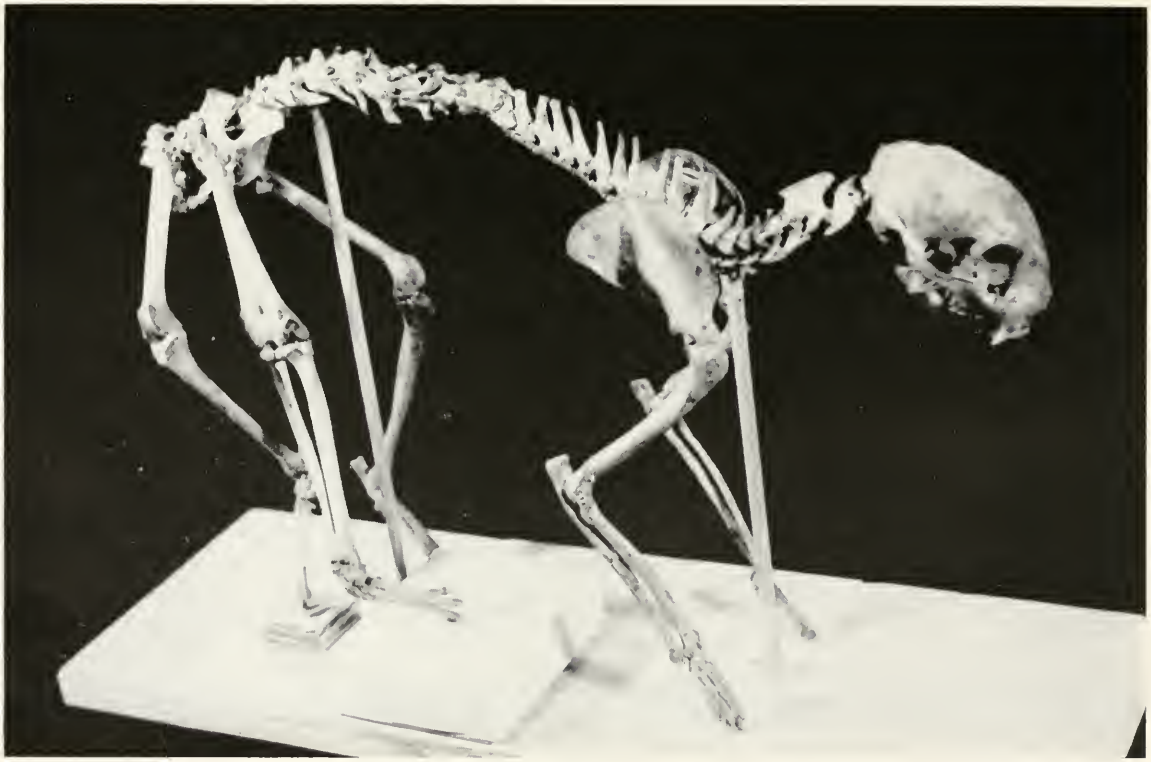

PLATE 1

PLATE 2

PLATE 2. X-ray of the posterior part of the cat showing the regular right and teratological hind limbs in lateral view. x$^2/_3$.

PLATE 2

PLATE 3

PLATE 3. A, snapshot of the cat in life. B and C, teratological foot in ventral (normal dorsal) and dorsal (normal plantar) views. B and C x4/5.

A

B

C

PLATE 3

PLATE 4

PLATE 4. Teratological foot in lateral view compared to a normal left foot in dorsal view. x6/5.

PLATE 4

Bulletin of the Museum of Comparative Zoology
AT HARVARD COLLEGE
Vol. 114, No. 7

POST-TRIASSIC NAUTILOID GENERA

By Bernhard Kummel

With Twenty-eight Plates

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
August, 1956

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TABLE OF CONTENTS

	Page
Introduction	324
Classification of Post-Triassic Nautiloids	325
Evolution	344
Systematic Paleontology	360
Family Nautilidae d'Orbigny, 1840	360
Subfamily Nautilinae d'Orbigny, 1840	361
Genus *Cenoceras* Hyatt, 1883	361
Genus *Eutrephoceras* Hyatt, 1894	377
Genus *Pseudocenoceras* Spath, 1927	384
Genus *Carinonautilus* Spengler, 1910	385
Genus *Obinautilus* Kobayashi, 1954	386
Genus *Nautilus* Linné, 1758	387
Subfamily Pseudaganidinae nov.	389
Genus *Pseudaganides* Spath, 1927	390
Genus *Pseudonautilus* Meek, 1876	397
Subfamily Paracenoceratinae Spath, 1927	399
Genus *Paracenoceras* Spath, 1927	402
Genus *Aulaconautilus* Spath, 1927	409
Genus *Tithonoceras* Retowski, 1894	410
Genus *Somalinautilus* Spath, 1927	411
Subfamily Cymatoceratinae Spath, 1927	412
Genus *Cymatoceras* Hyatt, 1884	417
Genus *Paracymatoceras* Spath, 1927	427
Genus *Procymatoceras* Spath, 1927	428
Genus *Cymatonautilus* Spath, 1927	430
Genus *Anglonautilus* Spath, 1927	430
Genus *Eucymatoceras* Spath, 1927	431
Genus *Syrionautilus* Spath, 1927	433
Genus *Heminautilus* Spath, 1927	434
Genus *Deltocymatoceras* n.gen.	438
Genus *Epicymatoceras* n.gen.	439
Subfamily Hercoglossinae Spath, 1927	440
Genus *Cimomia* Conrad, 1866	445
Genus *Angulithes* Montfort, 1808	452
Genus *Hercoglossa* Conrad, 1866	457

Page

Genus *Aturoidea* Vredenburg, 1925 462
Subfamily Aturinae Hyatt, 1894 464
Genus *Aturia* Bronn, 1838 464
Addendum 468
Bibliography 469

ILLUSTRATIONS

PLATES

Plate

1. *Cenoceras orbignyi* .....
2. *Cenoceras trechmanni* .....
3. *Cenoceras striatus* .....
4. *Cenoceras simillimus* .....
5. *Cenoceras inornatus* .....
6. *Cenoceras burtonensis* .....
7. *Cenoceras* and *Syrionautilus* .....
8. *Paracenoceras* and *Cenoceras* .....
9. *Obinautilus* and *Cenoceras* .....
10. *Heminautilus* and *Pseudocenoceras* .....
11. *Carinonautilus ariyalurensis* .....
12. *Pseudonautilus geinitzi* .....
13. *Paracenoceras hexagonum* .....
14. *Aulaconautilus* and *Somalinautilus* .....
15. *Tithonoceras zitteli* .....
16. *Cymatoceras pseudoelegans* .....
17. *Procymatoceras subtruncatus* .....
18. *Cymatonautilus julii* .....
19. *Paracymatoceras asper* .....
20. *Anglonautilus undulatus* .....
21. *Eucymatoceras plicatus* .....
22. *Deltocymatoceras leiotropis* .....
23. *Epicymatoceras vaelsensis* .....
24. *Cimomia burtini* .....
25. *Angulithes* and *"Bisiphytes"* .....
26. *Angulithes triangularis* .....
27. *Hercoglossa orbiculata* .....
28. *Aturoidea* and *Pseudaganides* .....

FIGURES

Figure		Page
1.	Bar chart of nautiloid genera per period	345
2.	Phylogenetic relationships of late Triassic and early Jurassic nautiloids	347
3.	Phylogeny of post-Triassic nautiloids	348
4.	Bar chart of number of genera of post-Triassic nautiloids per series	353
5.	Bar chart of number of species of post-Triassic nautiloids per series	357
6.	Distribution map of *Cenoceras*	358
7.	Distribution map of *Eutrephoceras*	359
8.	*Cenoceras*	363
9.	*Cenoceras*	365
10.	*Cenoceras*	367
11.	*Cenoceras excavatus*	369
12.	*Cenoceras burtonensis*	371
13.	*Eutrephoceras*	378
14.	*Pseudaganides*	391
15.	*Pseudaganides* and *Pseudonautilus*	393
16.	*Permoceras* and *Pseudonautilus*	399
17.	Distribution map of Paracenoceratinae	401
18.	*Paracenoceras hexagonum*	403
19.	*Paracenoceras* and *Aulaconautilus*	404
20.	*Paracenoceras* and *Heminautilus*	406
21.	Distribution map of Lower Cretaceous Cymatoceratinae	414
22.	Distribution map of Upper Cretaceous Cymatoceratinae	415
23.	*Cymatoceras, Paracymatoceras, Deltocymatoceras, Procymatoceras, Epicymatoceras*	419
24.	*Cymatoceras* and *Paracymatoceras*	422
25.	*Procymatoceras subtruncatus*	429
26.	*Anglonautilus undulatus*	431
27.	*Eucymatoceras plicatus*	432
28.	*Heminautilus saxbii*	436
29.	Distribution map of Cretaceous Hercoglossinae	442
30.	Distribution map of Tertiary Hercoglossinae	443
31.	*Hercoglossa, Cimomia,* and *Aturoides*	446
32.	*Cimomia* and *Angulithes*	448
33.	*Angulithes*	454
34.	*Hercoglossa* and *Aturoidea*	458
35.	Distribution map of Aturinae	465

INTRODUCTION

Studies on tetrabranchiate cephalopods have added much data to our understanding of the patterns and modes of evolution as displayed by fossil animals. Few invertebrate phyla show such marked periods of expansion in evolutionary intensity contrasted with periods of extreme contraction to the point of near extinction. The generalized evolutionary history of the ammonoids with periods of near extinction at the end of the Paleozoic and again at the end of the Triassic, and their final extinction at the end of the Cretaceous is well known. Among the nautiloid cephalopods a similar evolutionary history exists but with some important differences.

The nautiloid cephalopods had their greatest radiation soon after their first appearance in the Upper Cambrian, that is in the Ordovician. In this early phase of their history numerous distinct phyletic trends are well established. However, by Silurian time there is already a marked decline in the number of genetic groups. This decline in the viability of the nautiloids continued, until today we have only a single genus (*Nautilus*) living as a relic form in the southwest Pacific. In this long, gradually diminishing diversity the nautiloids nearly became completely extinct in the late Triassic, a period of extinction coinciding with a similar phase in the evolution of the ammonoids. A single stock derived from the Triassic Syringonautilidae survived into the Jurassic. From this surviving stock all post-Triassic nautiloids are directly or indirectly derived.

The purpose of this study is to analyze the evolutionary history of the family Nautilidae which includes the surviving stock from the Triassic and all post-Triassic nautiloid genera. This phyletic group is of particular interest since it includes an evolutionary complex which has survived a period of near extinction of the class, went through a minor eruptive phase in the development of new adaptive types, and is now represented by a single genus. No explanation is given as to the cause of the

decreasing viability of the nautiloids, but the patterns and modes of evolution of this declining group are instructive.

Post-Triassic nautiloids have received but scant attention, most workers having merely referred all species to the genus *Nautilus*. In 1927, L. F. Spath presented a very comprehensive, but short, review of post-Triassic nautiloids and proposed a taxonomic scheme including many new genera. In 1951, I spent eight months at the British Museum of Natural History, and at that time had the opportunity of studying the very large and excellent collections of that institution including the types of many of the genera proposed by Spath. At the time Spath (1927a) proposed his taxonomic scheme for post-Triassic nautiloids he did not give any diagnosis of his genera or illustrations of his type species, many based on Sowerby species not previously illustrated except in woodcuts. In the present report all genera of post-Triassic nautiloids are diagnosed and illustrated. An intensive search has been made of the literature to bring together, as far as possible, all species names that have been proposed over the past hundred odd years. In this way data was obtained on the variability, geologic range and geographic distribution of each generic group.

This study is an outgrowth of the preparation of a chapter on Mesozoic nautiloids for the Treatise on Invertebrate Paleontology, edited by R. C. Moore. A similar study on Carboniferous to Triassic nautiloids has already been published (Kummel, 1953c). I wish to express my very sincere appreciation to Dr. L. F. Spath for many long hours of stimulating conversations and for facilitating in every way my work at the British Museum. Fruitful discussions with Dr. Curt Teichert and Dr. Ernest Williams on taxonomic and evolutionary problems were most helpful.

CLASSIFICATION OF POST-TRIASSIC NAUTILOIDS

The only previous comprehensive discussion of post-Triassic nautiloids is that of L. F. Spath (1927a). In recent years several large works on Tertiary nautiloids have been produced by Miller which have included descriptions of many new Tertiary faunas. Spath's discussion of post-Triassic nautiloids was only a small and incidental part of his brilliant work on the famous Jurassic

fauna of Kachh (Cutch). Even so, he laid the framework for future work on these animals.

Nautiloids of Mesozoic age and, until recently, Tertiary age have received only brief incidental treatment in paleontological publications. For one thing post-Triassic nautiloids are not common fossils compared to the contemporaneous ammonoid, pelecypod, or gastropod faunas. They likewise are seemingly not nearly so diverse. The evolutionary decline of the nautiloids, already very marked in the Silurian, progresses steadily towards the Recent. Thus in studying Mesozoic and Tertiary nautiloids we are closely examining the decline and near extinction of a large animal group.

Until the contribution by Spath (1927a) there had been few genera proposed for post-Triassic nautiloids and most of these were not generally accepted or used. The most common practice was to place all post-Triassic species in the genus *Nautilus*. Those genera that had been proposed before Spath's 1927 revision include *Nautilus* Linné, 1758, *Bisiphytes* Montfort, 1808, *Cenoceras* Hyatt, 1883, *Eutrephoceras* Hyatt, 1894, *Digonioceras* Hyatt, 1894, *Angulithes* Montfort, 1808, *Hercoglossa* Conrad, 1866, *Pseudonautilus* Meek, 1876, *Cimomia* Conrad, 1866, *Cymatoceras* Hyatt, 1883, *Tithonoceras* Retowski, 1893, *Carinonautilus* Spengler, 1910, and *Aturia* Bronn, 1838. As mentioned above, most of these genera were never used after their original proposal; however, such generic names as *Eutrephoceras, Hercoglossa, Cymatoceras,* and *Aturia* are fairly common in the early literature. Most of these genera were considered as members of the Nautilidae.

In his revision of post-Triassic nautiloids Spath (1927a) proposed 16 new genera and adopted 5 families, namely the Nautilidae d'Orbigny, 1840, the Hercoglossidae Spath, 1927, the Cymatoceratidae Spath, 1927, the Paracenoceratidae Spath, 1927, and the Aturidae Hyatt, 1894. On a straight morphological basis, the Nautilidae include those genera directly or indirectly in the main stock giving rise to *Nautilus*. The Hercoglossidae include those genera with "goniatitic" or very sinuous sutures. The Cymatoceratidae include those stocks characterized by ribbing — the only stock of post-Triassic nautiloids with any ornamentation. The Paracenoceratidae are characterized by differentiation of the periphery, and the Aturidae are characterized by

the unique and peculiar dorsal siphuncle.

There have been no significant changes made to this taxonomic arrangement since its proposal in 1927. Restudy of the large nautiloid collections in the British Museum and the Museum of Comparative Zoology plus a comprehensive review of the literature have brought forth further data on the range of variation within the various genera, and also new data on the geographic and stratigraphic range of most of the species described.

The nautiloids reflect no significant change in their evolutionary development from the late Paleozoic into the Triassic. In fact, the evolutionary pattern of Triassic nautiloids is merely a culmination of trends begun back in the Carboniferous (Kummel, 1953c). Towards the end of the Triassic most of the long-lived stocks became extinct. A single persisting stock represented by *Cenoceras* survived the Triassic, and it represents the root form from which, directly or indirectly, all post-Triassic nautiloids are derived. On examination of the available data on post-Triassic nautiloids, one is impressed by the essential homogeneity of the group. Distinctive radiations are recognizable, each representing an elaboration of particular morphological characters. Homeomorphous developments within the group and with pre-Jurassic genera are common. The time-space relationships of the post-Triassic nautiloid "species" and their morphological modifications, interpreted in terms of adaptive radiation, make possible a constructive phylogenetic interpretation of the group. The interpretation presented in this report gives a much clearer understanding of the various generic groups and the kinds and ranges of variation within the groups. The classification adopted reflects the phylogeny of post-Triassic to Recent nautiloids. The classification used in this report is as follows:

Family Nautilidae d'Orbigny, 1840
  Subfamily Nautilinae d'Orbigny
    Genus *Nautilus* Linné, 1758
      Type species: *Nautilus pompilius* Linné
    Genus *Cenoceras* Hyatt, 1883
      Type species: *Nautilus orbignyi* Prinz
    Genus *Eutrephoceras* Hyatt, 1894
      Type species: *Nautilus dekayi* Morton
    Genus *Pseudocenoceras* Spath, 1927
      Type species: *Nautilus largilliertianus* d'Orbigny

Genus *Carinonautilus* Spengler, 1910
Type species: *Carinonautilus ariyalurensis* Spengler
Genus *Obinautilus* Kobayashi, 1954
Type species: *Obinautilus pulchra* Kobayashi
Subfamily Pseudaganidinae nov.
Genus *Pseudaganides* Spath, 1927
Type species: *Nautilus kutchensis* Waagen
Genus *Pseudonautilus* Meek, 1876
Type species: *Nautilus geinitzi* Oppel
Subfamily Paracenoceratinae Spath, 1927
Genus *Paracenoceras* Spath, 1927
Type species: *Nautilus hexagonus* J. de C. Sowerby
Genus *Aulaconautilus* Spath, 1927
Type species: *Tautilus sexcarinatus* Pictet
Genus *Somalinautilus* Spath, 1927
Type species: *Nautilus antiquus* Dacqué
Genus *Tithonoceras* Retowski, 1894
Type species: *Tithonoceras zitteli* Retowski
Subfamily Cymatoceratinae Spath, 1927
Genus *Cymatoceras* Hyatt, 1883
Type species: *Nautilus pseudoelegans* d'Orbigny
Genus *Procymatoceras* Spath, 1927
Type species: *Nautilus subtruncatus* Morris and Lycett
Genus *Cymatonautilus* Spath, 1927
Type species: *Nautilus julii* d'Orbigny
Genus *Paracymatoceras* Spath, 1927
Type species: *Nautilus asper* Oppel
Genus *Syrionautilus* Spath, 1927
Type species: *Nautilus libanoticus* Foord and Crick
Genus *Anglonautilus* Spath, 1927
Type species: *Nautilus undulatus* J. Sowerby
Genus *Eucymatoceras* Spath, 1927
Type species: *Nautilus plicatus* Fitton
Genus *Heminautilus* Spath, 1927
Type species: *Nautilus saxbii* Morris
Genus *Deltocymatoceras* n.gen.
Type species: *Nautilus leiotropis* Schlüter
Genus *Epicymatoceras* n.gen.
Type species: *Nautilus vaelsensis* Binckhorst
Subfamily Hercoglossinae Spath, 1927
Genus *Hercoglossa* Conrad, 1866
Type species: *Nautilus orbiculatus* Tuomey
Genus *Cimomia* Conrad, 1866
Type species: *Nautilus burtini* Galeotti

Genus *Angulithes* Montfort, 1808
Type species: *Nautilites triangularis* Montfort
Genus *Aturoidea* Vredenburg, 1925
Type species: *Nautilus parkinsoni* Edwards
Subfamily Aturinae Hyatt, 1894
Genus *Aturia* Bronn, 1838
Type species: *Nautilus aturi* Basterot

Because of the essential homogeneity of post-Triassic nautiloids their grouping into a single family — Nautilidae — seems most appropriate. Thus each of the distinctive radiations from the main evolving stock is reflected at the subfamily level and the radiations within the subfamilies are expressed at the generic level.

Several genera that have been proposed are considered to be synonyms of previously described forms. *Bisiphytes* Montfort, 1808, is suppressed because of the great ambiguity connected with the type species. *Sphaeronautilus* Spath, 1927, *Digonioceras* Hyatt, 1894, *Ophionautilus* Spath, 1927, and *Nautilites* Prinz, 1906, are considered to be synonyms of *Cenoceras*. *Hercoglossoceras* Spath, 1927, is considered to be a synonym of *Pseudaganides* Spath. The single species assigned to *Neocymatoceras* Kobayashi, 1954, falls within the range of variation of *Cymatoceras* and the genus is suppressed. *Vorticoceras* Scott, 1940, was established before its author knew of *Heminautilus* Spath, 1927, and was suppressed by Scott at a later date (Scott, 1943). *Platynautilus* Yabe and Ozaki, 1953, is a perfect synonym of *Heminautilus*. *Deltoidonautilus* Spath, 1927, is a synonym of *Angulithes* Montfort, 1808 (Kummel, 1953a). *Enclimatoceras* Hyatt, 1883, is a synonym of *Hercoglossa* Conrad, 1866 (Spath, 1927a). *Woodringia* Stenzel, 1940, also is here considered a synonym of *Hercoglossa*. *Paraturia* Spath (1927) was proposed prior to his (Spath's) knowledge of *Aturoidea* Vredenburg, 1925, and was shortly thereafter properly suppressed for *Aturoidea* which has priority.

The basic framework of the above classification is the work of Spath (1927a) but differs in some important aspects involving the general interpretation and phylogenetic relationships of post-Triassic nautiloids. Spath (1927a) originally proposed his major units as families, but later (1935b) he did use a subfamily rank while describing a species of *Paracenoceras* (Paraceno-

ceratinae). Within the Nautilinae the main difference in the above classification from that of Spath is placing *Angulithes* in the Hercoglossinae, and including *Carinonautilus* in the Nautilinae, which Spath had placed in the Paracenoceratinae. Also several genera of Spath's Nautilidae (*Bisiphytes, Sphaeronautilus, Digonioceras,* and *Ophionautilus*) are suppressed or placed in synonymy of other genera.

The Pseudaganidinae is a new subfamily proposed to differentiate those nautiloids with sinuous sutures that arose as a separate phyletic stock in the early Jurassic, and are distinct from the Cretaceous-Tertiary radiation including *Hercoglossa* etc. Spath (1927a) had included the two genera of the Pseudaganidinae (*Pseudaganides* and *Pseudonautilus*) in the Hercoglossidae. From Spath's Paracenoceratidae are removed *Carinonautilus* to the Nautilinae and *Hominautilus* to the Cymatoceratinae. The subfamily Aturinae includes only the genus *Aturia*. The Cymatoceratinae remains essentially as conceived by Spath except for the inclusion of *Hominautilus* and two new genera described in this report.

The relative rarity of post-Triassic nautiloids has led to a situation where most species have been described on the basis of one or very few specimens. To my knowledge, no large collection representing a population has ever been assembled from a single horizon and locality nor are any known where the fossils are sufficiently well preserved to allow a thorough study of intraspecific variation. The great majority of species are defined in terms of being slightly thinner, fatter or more involute or evolute than other already established species; or there are slight variations in the whorl shape or character of the suture. However, in none of these species is the range of variations in any of their morphological features known. Because of these factors, the so-called species of Mesozoic and Tertiary nautiloids have little reality in terms of our concepts of neontological species. Thus, in attempting to decipher the evolutionary patterns and modes of these nautiloids, it is impossible to use the species as a working unit. One's thinking and correlation of data need to be at the generic level. The species (representing the named units accumulated in the literature) when brought together in generic groups give very useful data in regard to range and direction of variation, and relative abundance of the various

adaptive types. Since so many of the so-called species are merely descriptions of specimens, they are here treated as examples of morphologic types brought together into genera — which are the only feasible taxonomic units to handle with this sort of material. Another difficulty is the complete lack of understanding of the adaptive values of the various morphological features. Most features of the conch are thought to be adaptive, but the exact nature of this adaptation is not known.

To properly appraise the evolutionary history of post-Triassic nautiloids it was essential that all of the named units be brought together and placed in generic groups. Thus, through the named units (species), the geologic history and range of variation, origin, and evolution of each generic group could be interpreted in terms of the whole nautiloid fauna. In assembling a list of described species, there are numerous problems of synonymy and other taxonomic irregularities that cannot possibly be determined just from the literature, and it is doubtful at this stage if such efforts would be worthwhile. Thus in compiling a list of the species of post-Triassic nautiloids most names that have been introduced are listed, except for several very obvious and long recognized cases of synonymy. The following list of 531 species of post-Triassic nautiloids gives the units upon which much of this study is based. Because of the great difficulty in tracking down many of these forms the author, date, original generic assignment, and the present generic assignment are given. The list is reasonably complete but even after several years of accumulating these data it is certain that there are still species that have escaped my attention. This list of forms does represent the great majority and from it certain interesting observations on relative abundance of the various adaptive types can be made. This problem will be discussed later.

SPECIES OF POST-TRIASSIC NAUTILOIDS

Nautilus (Paracenoceras) acklini Jeannet, 1951 — *Paracenoceras*
N. adneticus Pia, 1914 — *Cenoceras*
N. (Hercoglossa) aegyptiacus Foord, 1891 — *Angulithes*
N. affinis Chapuis and Dewalque, 1853 — *Cenoceras*
N. aganiticus Schlotheim, 1820 — *Pseudaganides*
N. ahltenensis Schlüter, 1876 — *Eutrephoceras*
N. alabamensis Morton, 1834 — *Aturia*

Aturia alaskensis Schenck, 1931 — *Aturia*
N. albensis d'Orbigny, 1850 — *Cymatoceras*
Eutrephoceras alcesense Reeside, 1927 — *Eutrephoceras*
N. allani Fleming, 1945 — *Eutrephoceras*
N. allioni Michelotti, 1840 — *Eutrephoceras*
N. altarensis Pomel, 1889 — *Cymatoceras*
N. altifrons Chapman, 1915 — *Eutrephoceras*
N. altisiphites Prinz, 1906 — *Cenoceras*
N. amasianus Gugenberger, 1928 — *Cenoceras*
N. ammoni Loesch, 1912 — *Pseudaganides*
N. amorettii Parona, 1897 — *Cenoceras*
Cymatoceras andranofotsyense Collignon, 1951 — *Cymatoceras*
N. angulifcrous Schlüter, 1876 — *Cymatoceras*
N. angustata Conrad, 1849 (*in* Dana) — *Aturia*
N. angustus Blanford, 1861 — *Cimomia*
N. anomphalus Pia, 1914 — *Cenoceras*
N. antiquus Dacqué, 1910 — *Somalinautilus*
N. applanatus Wanner, 1902 — *Pseudocenoceras*
N. arariformis Pia, 1914 — *Cenoceras*
N. araris Dumortier, 1869 — *Cenoceras*
N. aratus Quenstedt, 1846 — *Cenoceras*
N. archiacianus d'Orbigny, 1840 — *Eutrephoceras*
N. arcuatus Deshayes (*in* Leymerie, 1842) — *Angulithes*
N. arduennensis Loesch, 1914 — *Paracenoceras*
N. argovicnsis Loesch, 1912 — *Pseudaganides*
Carinonautilus ariyalurensis Spengler, 1910 — *Carinonautilus*
N. arthaberi Gugenberger, 1928 — *Cenoceras*
N. articulatus Pulteney, 1813 (*in* Cox, 1940) — *Cymatoceras*
N. asper Oppel, 1865 — *Paracymatoceras*
N. astacoides Young & Bird, 1828 — *Cenoceras*
N. atlas Whiteaves, 1876 — *Cymatoceras*
N. aturi Basterot, 1825 — *Aturia*
N. aturioides Pictet, 1867 — *Pseudonautilus*
Aturia australis McCoy, 1867 — *Aturia*
N. austriacus Hauer, 1856 — *Cenoceras*
N. averilli Anderson, 1938 — *Cymatoceras* ?
N. baberi Morris & Lycett, 1850 — *Procymatoceras*
N. baconicus Vadász, 1911 — *Cenoceras*
Deltoidenautilus bakeri Teichert, 1947 — *Angulithes*
N. balcombensis Chapman, 1915 — *Eutrephoceras*
N. balsamocrivellii Parona, 1897 — *Cenoceras*
Aturia basteroti Benoist, 1888 — *Aturia*
N. bayfieldi Foord and Crick, 1890 — *Cymatoceras*

N. begudensis Kilian and Reboul, 1915 — *Anglonautilus*
N. bellerophon Lundgren, 1867 — *Eutrephoceras*
N. berriasensis Pictet, 1867 — *Pseudocenoceras*
Eutrephoceras berryi Miller, 1947 — *Eutrephoceras*
Aturia (Aturia) berryi Stenzel, 1940 — *Aturia*
N. (Aulaconautilus) bicarinatus Jeannet, 1951 — *Aulaconautilus*
N. bifurcatus Ooster, 1858 — *Cymatoceras*
Deltoidonautilus biyogorensis Haas and Miller, 1952 — *Angulithes*
N. blakei Avnimelech, 1947 — *Cimomia*
N. blanfordi Douvillé, 1929 — *Eutrephoceras*
N. bodeni Loesch, 1914 — *Pseudaganides*
N. boissieri Pictet, 1867 — *Eutrephoceras*
N. bouchardianus d'Orbigny, 1840 — *Eutrephoceras*
N. bradfordensis Crick, 1898 — *Cenoceras*
N. brancoi Gemmellaro, 1884 — *Cenoceras*
Aturia (Brazaturia) brazoensis Stenzel, 1935 — *Aturia*
N. breislacki Parona, 1897 — *Cenoceras*
N. broitzemensis Müller and Wollemann, 1906 — *Cymatoceras*
Aturia (Sphenaturia) brüggeni Ihering, 1921 — *Aturia*
N. brunhuberi Loesch, 1914 — *Pseudaganides*
Aturia brunlechneri Frauscher, 1895 — *Aturoidea*
N. bruntrutanae Kuhn, 1936 — *Paracenoceras*
N. bryani Gabb, 1877 — *Eutrephoceras*
Cimomia buccinaeformis Haas and Miller, 1952 — *Cimomia*
N. burkarti Castillo and Aguilera, 1895 — *Eutrephoceras*
N. burtini Galeotti, 1837 — *Cimomia*
N. burtonensis Foord and Crick, 1890 — *Cenoceras*
N. butonensis Martin, 1933 — *Eutrephoceras*
Deltoidonautilus caheni Miller, 1951 — *Angulithes*
N. calloviensis Oppel, 1858 — *Paracenoceras*
N. calvimontensis Bédé, 1948 — *Angulithes*
N. campbelli Meek, 1861 — *Cymatoceras* ?
N. campichei Karakasch, 1907 — *Pseudocenoceras*
N. cantabrigiensis Foord, 1891 — *Cimomia*
N. (Cymatoceras) carlottensis Whiteaves, 1900 — *Cymatoceras*
N. caroliameghinoi Ihering, 1902 — *Aturia*
Eutrephoceras carolinense Kellum, 1926 — *Eutrephoceras*
N. (Hercoglossa) cassinianus Foord and Crick, 1890 — *Angulithes*
N. catonis Gemmellaro, 1886 — *Cenoceras*
N. cenomanensis Schlüter, 1876 — *Cymatoceras*
N. centralis J. Sowerby, 1812 — *Eutrephoceras*
Aturia charlesworthi Foord, 1891 — *Aturia*
N. charpentieri Leymerie, 1851 — *Eutrephoceras*

N. chilensis Huppé (*in Gay*) 1854 — *Cenoceras*
N. chudeaui Douvillé, 1920 — *Angulithes*
Aturia clarkei Teichert, 1944 — *Aturia*
N. clausus d'Orbigny, 1842 — *Pseudaganides*
N. clementinus d'Orbigny, 1840 — *Eutrephoceras*
Cymatoceras colombiana Durham, 1946 — *Cymatoceras*
N. columbinus Fritsch and Schlönbach, 1872 — *Cimomia*
N. compressus Tavani, 1942 — *Cymatoceras*
N. cookana Whitfield, 1892 — *Eutrephoceras*
N. cossmanni Vredenburg, 1928 — *Cimomia*
Paracenoceras costatum Scott, 1943 — *Procymatoceras*
Aturia ? coxi Miller, 1947 — *Aturia*
N. crassiconcha Vogl, 1908 — *Cimomia*
N. crassisinuatus Crick, 1898 — *Pseudaganides*
N. crassus Schafhäutl, 1863 — *Eutrephoceras*
N. crebricostatus Blanford, 1861 — *Cymatoceras*
N. cubaensis Lea, 1841 — *Aturia*
Aturia curvilineata Miller and Thompson, 1937 — *Aturia*
N. cyclotus Oppel, 1865 — *Eutrephoceras*
N. danicus Schlotheim, 1820 — *Hercoglossa*
Eutrephoceras dartevellei Miller, 1951 — *Eutrephoceras*
N. darupensis Schlüter, 1876 — *Eutrephoceras*
N. decipiens Michelotti, 1861 — *Eutrephoceras*
N. dekayi Morton, 1834 — *Eutrephoceras*
N. deluci d'Archiac 1854 — *Angulithes*
N. demonensis M. Gemmellaro, 1911 — *Cenoceras*
N. depressus Binckhorst, 1861 — *Eutrephoceras*
N. desertorum Quaas, 1902 — *Eutrephoceras*
N. deslongchampsianus d'Orbigny, 1840 — *Cymatoceras*
Aturia dickersoni Schenck, 1931 — *Aturia*
Hercoglossa diderrichi Vincent, 1913 — *Hercoglossa*
N. dietrichi Zwierzycki, 1914 — *Eutrephoceras*
N. (Paracenoceras) dilatatus Jeannet, 1951 — *Paracenoceras*
N. dispansus Morris and Lycett, 1850 — *Cenoceras ?*
Aturoidea distans Teichert, 1943 — *Aturoidea*
N. distefanoi Gemmellaro, 1884 — *Cenoceras*
N. divesianus Kuhn, 1936 — *Paracenoceras*
N. domeykus d'Orbigny, 1842 — *Cenoceras*
N. d'orbignyanus Forbes, 1846 — *Cimomia*
N. dorsatus Roemer, 1836 — *Paracenoceras*
N. dorsoexcavatum Parona and Bonarelli, 1897 — *Paracenoceras*
Eutrephoceras douvillei Spath, 1927 — *Eutrephoceras*
N. drepanensis Tagliarini, 1901 — *Pseudaganides*

N. dubaleni Peyrot, 1932 — *Eutrephoceras*
N. dubius Zieten, 1830 — *Cenoceras*
N. duilii Gemmellaro, 1886 — *Pseudaganides*
N. dumasi Pictet, 1867 — *Pseudaganides*
N. egregius Pia, 1914 — *Cenoceras*
N. eichwaldi Karakasch, 1907 — *Cymatoceras*
N. elegans J. Sowerby, 1816 — *Cymatoceras*
N. elegantoides d'Orbigny, 1840 — *Cymatoceras*
Deltoidonautilus elliotti Stenzel, 1940 — *Angulithes*
N. ellipticus Schafhäutl, 1852 — *Cimomia*
N. emmianum Dacqué, 1905 — *Paracenoceras*
N. ercycinus Tagliarini, 1901 — *Cenoceras*
Heminautilus etheringtoni Durham, 1946 — *Heminautilus*
N. euthymi Pictet, 1867 — *Eutrephoceras*
N. excavatus, J. de C. Sowerby, 1826 — *Cenoceras*
N. exiguus Crick, 1898 — *Cenoceras*
N. expansus J. de C. Sowerby, 1824 — *Eutrephoceras*
N. expletus Zwierzycki, 1914 — *Cimomia*
N. exterebratus Crick, 1898 — *Cenoceras*
Eutrephoceras fuxoense Hyatt, 1894 — *Eutrephoceras*
N. felix Chapman, 1915 — *Eutrephoceras*
Aturia (Sphenaturia) felschi Ihering, 1921 — *Aturia*
N. fischeranus Foord and Crick, 1890 — *Cenoceras*
N. fittoni Sharpe, 1853 — *Pseudocenoceras*
N. flammeus Ronchetti, 1947 — *Eutrephoceras*
N. fleuriausianus d'Orbigny, 1840 — *Angulithes*
N. forbesi d'Archiac and Haime, 1854 — *Cimomia*
N. forbesianus Blanford, 1861 — *Hercoglossa* ?
Aturia formae Parona, 1899 — *Aturia*
N. formosus Blanford, 1861 — *Cymatoceras*
N. fourneti Dumortier, 1874 — *Cenoceras*
N. francomontanus Kuhn, 1939 — *Eutrephoceras*
N. franconicus Oppel, 1865 — *Pseudaganides*
N. (Pseudaganides) frickensis Jeannet, 1951 — *Pseudaganides*
N. fuscus Crick, 1898 — *Somalinautilus*
N. gabbi Anderson, 1902 — *Cymatoceras*
N. galea Fritsch and Schlönbach, 1872 — *Angulithes*
N. galicianus Alth, 1850 — *Pseudocenoceras*
Hercoglossa gardnerae Stenzel, 1940 — *Hercoglossa*
Aturia (Brazaturia) garretti Stenzel, 1940 — *Aturia*
N. geelongensis Foord, 1891 — *Eutrephoceras*
N. geinitzi Oppel, 1865 — *Pseudonautilus*
N. geyeri Prinz, 1906 — *Cenoceras*

N. giganteus d'Orbigny, 1825 — *Paracenoceras*
N. girardoti de Loriol, 1903 — *Pseudaganides*
N. glaber Foord and Crick, 1890 — *Pseudaganides*
N. gosavicus Redtenbacher, 1873 — *Eutrephoceras*
Aturia grandior Schenck, 1931 — *Aturia*
Aturia (Aturia) grangei Fleming, 1945 — *Aturia*
N. granulosum d'Orbigny, 1843 — *Paracenoceras*
N. gravesianus d'Orbigny, 1843 — *Pseudaganides*
N. guilielmi telli Ooster, 1858 — *Cymatoceras*
N. hallidayi Waring, 1914 — *Eutrephoceras* ?
N. hallstattensis Spengler, 1919 — *Cenoceras*
N. haltomi Aldrich, 1931 — *Cimomia*
Eutrephoceras hannai Vokes, 1937 — *Eutrephoceras*
Hercoglossa harrisi Miller and Thompson, 1937 — *Hercoglossa*
N. haughti Olsson, 1928 — *Cimomia*
N. hazaracnsis Das-Gupta, 1916 — *Angulithes*
N. heberti Binckhorst, 1861 — *Cimomia*
N. helveticus Loesch, 1914 — *Pseudaganides*
N. (Cymatoceras?) hendersoni Etheridge (1901) — *Eutrephoceras*
N. (Paracenoceras) herznachensis Jeannet, 1951 — *Paracenoceras*
Cimomia hesperia Miller and Downs, 1950 — *Cimomia*
Paracenoceras hexagonoides Spath, 1927 — *Paracenoceras*
N. hexagonus J. de C. Sowerby, 1826 — *Paracenoceras*
N. hilli Shattuck, 1903 — *Cymatoceras*
N. hunstantonensis Foord and Crick, 1890 — *Cymatoceras*
Cimomia hunti Haas and Miller 1952 — *Cimomia*
N. huxleyanus Blanford, 1861 — *Cymatoceras*
N. imbricatus Crick, 1907 — *Cymatoceras*
Bisiphytes (Cenoceras) imlayi Kummel, 1954 — *Cenoceras*
N. impendens Crick, 1898 — *Cenoceras*
N. imperialis J. Sowerby, 1812 — *Cimomia*
N. indicum Spengler, 1910 — *Eutrephoceras*
Hercoglossa innominanda Fleming, 1945 — *Hercoglossa*
N. inornatus d'Orbigny, 1842 — *Cenoceras*
N. intermedius J. Sowerby, 1816 — *Cenoceras*
N. interstriatus Strombeck, 1863 — *Cymatoceras*
N. intumescens Waagen, 1873 — *Procymatoceras* ?
N. (Javanoceras) intuscatenatus Martin, 1932 — *Cimomia*
N. izumoensis Yokoyama, 1913 — *Eutrephoceras*
N. japonicus Shimizu, 1926 — *Eutrephoceras*
N. javanus Martin, 1879 — *Eutrephoceras*
Paracenoceras jeanneti Sanchez Roig, 1951 — *Paracenoceras*
Eutrephoceras johnsoni Miller, 1947 — *Eutrephoceras*

Eutrephoceras jonesi Miller and Thompson, 1933 — *Eutrephoceras*
N. jordani Wanner, 1902 — *Cimomia*
N. jourdani Dumortier, 1874 — *Cenoceras*
N. julianus Fucini, 1895 — *Cenoceras*
N. julii d'Orbigny, 1850 — *Cymatonautilus*
N. jumarensis Waagen, 1873 — *Paracenoceras* ?
N. jurensis Quenstedt, 1858 — *Cenoceras*
N. justus Blanford, 1861 — *Eutrephoceras*
Cimomia karkarensis Haas and Miller 1952 — *Cimomia*
N. karpinskyi Karakasch, 1907 — *Paracymatoceras*
N. kayeanus Blanford, 1861 — *Cymatoceras*
Aturia kerniana Anderson and Hanna, 1925 — *Aturia*
N. klebelsbergi Loesch, 1914 — *Pseudaganides*
Aganides kochi Prinz, 1906 — *Pseudaganides*
Aturia koenei Cagel, 1928 — *Aturia*
N. (Cymatoceras) kossmati Spengler, 1910 — *Cymatoceras*
N. krenkeli Jeannet, 1951 — *Pseudaganides*
Cimomia kugleri Miller, 1947 — *Cimomia*
N. kumagunense Waagen, 1873 — *Paracenoceras*
N. kutchensis Waagen, 1873 — *Pseudaganides*
N. labechei d'Archiac and Haime, 1854 — *Eutrephoceras*
N. lallierianus d'Orbigny, 1840 — *Heminautilus*
N. lamarckii Deshayes, 1824 — *Angulithes*
Hercoglossa lamegoi Oliveira, 1953 — *Hercoglossa*
N. landanensis Vincent, 1913 — *Cimomia*
N. largilliertianus d'Orbigny, 1840 — *Pseudocenoceras*
Aturia (Brazaturia) laticlavia Stenzel, 1935 — *Aturia*
N. latifrons Zwierzycki, 1914 — *Paracenoceras*
Eutrephoceras laverdei Durham, 1946 — *Eutrephoceras*
N. ledonicus de Loriol, 1903 — *Pseudaganides*
N. lehardyi Binckhorst, 1861— *Pseudocenoceras* ?
N. leiotropis Schlüter, 1876 — *Deltocymatoceras*
Deltoidonautilus lemoinei Miller, 1951 — *Angulithes*
N. lentiformis Stoliczka, 1866 — *Eutrephoceras*
N. leonei Negri, 1934 — *Eutrephoceras*
N. leonicensis de Zigno, 1881 — *Cimomia*
N. libanoticus Foord and Crick, 1890 — *Syrionautilus*
N. lineatus J. Sowerby, 1813 — *Cenoceras*
N. lineolatus Foord and Crick, 1890 — *Cenoceras*
Aturia linicentensis Vincent, 1907 — *Aturia* ?
Cymatoceras loeblichi Miller and Harris, 1945 — *Cymatoceras*
N. loricatus Schlüter, 1876 — *Cymatoceras*
Aturia lotzi Böhm, 1913 — *Aturia*

Aturia luculoensis Miller, 1938 — *Aturia*
Bisiphytes (Cenoceras) lupheri Kummel, 1954 — *Cenoceras*
N. lutatii Gemmellaro, 1886 — *Cenoceras*
Cimomia macfadyeni Haas and Miller, 1952 — *Cimomia*
Aturia (Brazaturia) mackayi Fleming, 1945 — *Aturia*
N. macrocephalus Schafhäutl, 1863 — *Cimomia*
N. (Cymatoceras) madagascarensis Yabe and Shimizu, 1924 — *Cymatoceras*
Hercoglossa madgascariensis Collignon, 1951 — *Hercoglossa*
N. malbosi Pictet, 1867 — *Pseudonautilus*
N. malherbii Terquem, 1855 — *Cenoceras*
N. manissadjiani Gugenberger, 1928 — *Cenoceras*
N. manuanensis Crick, 1907 — *Cymatoceras*
Hercoglossa maracaiboensis Miller and Collinson, 1951 — *Hercoglossa*
N. mariani M. Gemmellaro, 1911 — *Cenoceras*
N. marii Gemmellaro, 1886 — *Cenoceras*
Eutrephoceras marksi Miller, 1947 — *Eutrephoceras*
Paracenoceras marocense Miller and Collinson, 1952 — *Paracenoceras*
N. marucoensis Giovine, 1950 — *Eutrephoceras*
Cimomia marylandensis Miller and Thompson, 1933 — *Cimomia*
Aturia mathewsonii Gabb, 1864 — *Aturoidea*
N. mazzarensis Tagliarini, 1901 — *Cenoceras*
Hercoglossa meglameryae Miller and Thompson, 1933 — *Hercoglossa*
Hercoglossa merriami Dickerson, 1914 — *Hercoglossa*
N. metafleuriausi Douvillé, 1929 — *Eutrephoceras*
N. meyrati Ooster, 1858 — *Cenoceras*
N. mikado Krenkel, 1910 — *Cymatoceras*
Paracymatoceras milleri Humphrey, 1949 — *Paracymatoceras* ?
N. mjatschkowanus Loesch, 1914 — *Paracenoceras*
N. mojsisovicsi Neumayr, 1870 — *Cymatonautilus*
N. mokattamensis Foord, 1891 — *Cimomia*
N. molli Douvillé, 1920 — *Angulithes*
Eutrephoceras montanensis Kummel, 1954 — *Eutrephoceras*
N. montmollini Pictet and Campiche, 1859 — *Eutrephoceras*
N. morcaui d'Orbigny, 1842 — *Paracenoceras*
Aturia morrissi Michelotti, 1847 — *Aturia*
Paracenoceras mullerriedi Sanchez Roig, 1951 — *Paracenoceras*
N. multiseptatus Foord and Crick, 1890 — *Cenoceras*
N. munieri Choffat, 1886 — *Angulithes*
Aturia myrlae Hanna, 1927 — *Aturia*
Aturia narica Vredenburg, 1925 — *Aturia*
N. nebrascense Meek and Hayden, 1862 — *Cymatoceras*
N. neckerianus Pictet, 1847 — *Cymatoceras*
N. negama Blanford, 1861 — *Cymatoceras*

N. negritensis Olsson, 1928 — *Cimomia*
N. neocomiensis d'Orbigny, 1840 — *Cymatoceras*
N. neohispanicum Burckhardt, 1925 — *Cymatoceras*
N. neubergicus Redtenbacher, 1873 — *Eutrephoceras*
N. obesus J. Sowerby, 1816 — *Cenoceras*
N. obstructus Deslongchamps, 1878 — *Cenoceras*
Nautilus (Cymatoceras?) occlusus Crick, 1907 — *Cymatoceras*
Aturoidea olssoni Miller, 1947 — *Aturoidea*
N. oppeli Zittel, 1868 — *Pseudaganides*
N. orbiculatus Tuomey, 1854 — *Hercoglossa*
N. orbignyi Prinz, 1906 — *Cenoceras*
Eutrephoceras oregonense Miller, 1947 — *Eutrephoceras*
N. ornatus Foord and Crick, 1890 — *Cenoceras*
N. ornatus var. *atanatensis* Pia, 1914 — *Cenoceras*
Eutrephoceras ovoideum Crick, 1907 — *Eutrephoceras*
Aturia panamensis Miller, 1947 — *Aturia*
N. parabolicus Schafhäutl, 1863 — *Angulithes*
N. parallelus Schafhäutl, 1863 — *Cimomia*
N. paretoi M. Gemmellaro, 1911 — *Cenoceras*
N. parisiensis Deshayes, 1866 — *Eutrephoceras*
N. parkinsoni Edwards, 1849 — *Aturoidea*
Aturia paronai Rovereto, 1900 — *Aturia*
N. patens Kner, 1850 — *Cymatoceras*
N. paucifex Cope, 1866 — *Aturoidea*
N. parlowi Arkhanguelsky, 1904 — *Hercoglossa*
N. pellerensis Vialli, 1937 — *Pseudaganides*
N. perinflatus Foord and Crick, 1890 — *Cenoceras*
N. perlatus Morton, 1834 — *Eutrephoceras*
N. pernambucensis Maury, 1930 — *Cimomia*
N. perornatus Crick, 1894 — *Cenoceras*
N. perstriatus Steuer, 1921 — *Cymatoceras*
N. pertextus Dumortier, 1867 — *Cenoceras*
Aturia peruviana Olsson, 1928 — *Aturia*
Hercoglossa peruviana Berry, 1923 — *Hercoglossa*
N. (Hercoglossa) phosphaticus Bédé, 1933 — *Cimomia*
N. pictcti Karakasch, 1907 — *Pseudocenoceras*
N. pictcti Oppel 1865 — *Aulaconautilus*
N. piersantii Sergio, 1933 — *Eutrephoceras*
Aturoidea pilsbryi Miller and Thompson, 1935 — *Aturoidea*
N. pisanus Fucini, 1895 — *Cenoceras*
Eutrephoceras planoventer Stephenson, 1941 — *Eutrephoceras*
N. plicatus Fitton, 1835 — *Eucymatoceras*
N. polygonalis J. de C. Sowerby, 1826 — *Cenoceras*
Hercoglossa popenoei Miller and Downs, 1950 — *Hercoglossa*

N. portlandicus Foord and Crick, 1890 — *Pseudaganides*
N. postriatus Prinz, 1906 — *Cenoceras*
Aturia praeziczac Oppenheim, 1903 — *Aturia*
Aturia preaturi (Cuvillier) 1935 — *Aturia*
N. profundisiphites Prinz, 1906 — *Cenoceras*
Paracenoceras prohexagonum Spath, 1935 — *Paracenoceras*
N. (Cymatoceras) pseudoatlas Yabe and Shimizu, 1924 — *Cymatoceras*
N. pseudobouchardianus Spengler, 1910 — *Cimomia*
N. pseudoelegans d'Orbigny, 1840 — *Cymatoceras*
N. pseudolineatus Foord and Crick, 1890 — *Cenoceras*
N. (Cymatoceras) pseudonegama Spengler, 1910 — *Cymatoceras*
Cymatoceras pseudoneokomiense Shimizu, 1931 — *Cymatoceras*
N. pseudorugosus Pia, 1914 — *Cenoceras*
N. pseudotruncatus Crick, 1921 — *Cenoceras*
N. (Pseudaganides) pulchellus Jeannet, 1951 — *Pseudaganides*
Obinautilus pulchra Kobayashi, 1954 — *Obinautilus*
Cimomia pusilla Haas and Miller, 1952 — *Cimomia*
N. quadrangularis Pia, 1914 — *Cenoceras*
N. quadrilineatus Favre, 1869 — *Eutrephoceras*
Aturia radiata Bellardi, 1872 — *Aturia*
N. radiatus J. Sowerby, 1822 — *Cymatoceras*
N. rangei Hoppe, 1922 — *Heminautilus*
Eutrephoceras reesidei Stenzel, 1940 — *Eutrephoceras*
N. regalis J. de C. Sowerby, 1843 — *Eutrephoceras*
N. regularis Schafhäutl, 1863 — *Eutrephoceras*
N. restrictus Griepenkerl, 1889 — *Eutrephoceras*
N. resupinatus Redtenbacher, 1873 — *Eutrephoceras*
N. rhodani Roux, 1848 — *Paracenoceras*
Aturia richardsi Miller, 1947 — *Aturia*
N. ricordeanus d'Orbigny, 1847 (*in* Kilian and Reboul 1915) — *Hercoglossa*?
N. robustus Foord and Crick, 1890 — *Cenoceras*
N. roemeri Loesch, 1914 — *Pseudaganides*
Deltoidonautilus rogeri Miller, 1951 — *Angulithes*
N. rogeri Loesch, 1914 — *Pseudaganides*
N. rollandi Leymerie, 1846 — *Angulithes*
N. rollieri Loesch, 1914 — *Paracenoceras*
N. romeroi Ihering, 1903 — *Cimomia*
N. rota Blanford, 1861 — *Paracymatoceras*
Digonioceras rotundum Hyatt, 1894 — *Cenoceras*
N. rotundus Crick, 1898 — *Cenoceras*
Aturia rovasendiana Parona 1899 — *Aturia*
N. royeri de Loriol, 1872 — *Pseudaganides*
N. rugatus Fritsch and Schlönbach, 1872 — *Deltocymatoceras*
N. rugosus Buvignier, 1852 — *Cenoceras*

N. sahariensis Keller, 1932 — *Cimomia*
Cymatoceras sakalavum Collignon, 1949 — *Cymatoceras*
N. sanfilippoi Sorrentino, 1932 — *Eutrephoceras*
N. sattleri Krenkel, 1910 — *Paracenoceras*
N. saussureanus Pictet, 1847 — *Cymatoceras*
N. saxbii Morris, 1848 — *Hemina utilus*
N. seequrensis Tavani, 1942 — *Cymatoceras*
N. schattenbergi Kuhn, 1936 — *Paracenoceras*
N. schlosseri Loesch, 1914 — *Pseudaganides*
N. schlotheimi Loesch, 1914 — *Pseudaganides*
N. schlumbergeri Terquem, 1855 — *Cenoceras*
N. schmidti Giebel, 1852 — *Cenoceras*
N. schneidi Loesch, 1914 — *Pseudaganides*
N. schusteri Loesch, 1912 — *Paracenoceras*
N. schwalmi Prinz, 1906 — *Cenoceras*
N. schweinfurthi Quaas, 1902 — *Aturoidea*
N. schwertschlageri Loesch, 1912 — *Pseudaganides*
N. secernendus Pia, 1914 — *Cenoceras*
N. seelandi Penecke, 1884 — *Cimomia*
N. (Cymatoceras) semilobatus Spengler, 1910 — *Cymatoceras*
N. semiornatus Crick, 1898 — *Cenoceras*
N. semistriatus d'Orbigny, 1843 — *Cenoceras*
N. semiundatus Foord, 1891 — *Cymatoceras*
N. semseyi Prinz, 1904 — *Cenoceras*
N. senegalensis Douvillé, 1920 — *Angulithes*
Cimomia septemcastrensis Haas and Miller, 1952 — *Cimomia*
N. serpentinus Blanford, 1861 — *Aturoidea*
N. sexcarinatus Pictet, 1867 — *Aulaconautilus*
N. sharpei Schlüter, 1876 — *Cymatoceras*
N. sicilus Gemmellaro, 1868 — *Paracenoceras*
Hercoglossa simiensis Vokes, 1937 — *Hercoglossa*
Eutrephoceras simile Spath, 1953 — *Eutrephoceras*
N. simillimus Foord and Crick, 1890 — *Cenoceras*
N. sindiensis Vredenburg, 1928 — *Cimomia*
Deltoidonautilus singularis Haas and Miller, 1952 — *Angulithes*
N. sinuatoplicatus Geinitz, 1843 — *Cymatoceras ?*
N. sinuatus Sowerby, 1818 — *Pseudaganides*
N. sinuosus Roemer, 1836 — *Paracenoceras*
Eutrephoceras sloani Reeside, 1924 — *Eutrephoceras*
N. smithi Foord and Crick, 1890 — *Cenoceras*
N. somaliensis Newton, 1925 — *Angulithes*
Aturia somaliensis Haas and Miller, 1952 — *Aturia*
N. sowerbyanus d'Orbigny, 1840 — *Angulithes*
N. sowerbyi Wetherell, 1836 — *Angulithes*

Deltoidonautilus spathi Haas and Miller, 1952 — *Angulithes*
N. (Paraturia) spathi Vredenburg, 1928 — *Aturoidea*
N. sphaericus Forbes, 1846 — *Eutrephoceras*
Woodringia splendens Stenzel, 1940 — *Hercoglossa*
N. spreaficoi Parona, 1897 — *Cenoceras*
N. staadti Cossmann, 1902 — *Eutrephoceras*
N. staffelbergensis Kuhn, 1936 — *Paracenoceras*
Vorticoceras stantoni Scott, 1940 — *Heminautilus*
N. steinmanni Möricke, 1894 — *Cenoceras*
N. stephensoni Dickerson, 1914 — *Eutrephoceras*
N. steveni Karakasch, 1907 — *Eucymatoceras*
N. stoppanii Parona, 1897 — *Cenoceras*
N. strambergensis Oppel, 1865 — *Pseudaganides*
N. straticostatus Crick, 1907 — *Cymatoceras*
N. striatus J. Sowerby, 1817 — *Cenoceras*
N. stricteumbilicatus Stchépinsky, 1943 — *Eutrephoceras*
N. stromeri Loesch, 1914 — *Pseudaganides*
N. stschurouskii Milaschevitch, 1877 — *Eucymatoceras*
N. sturi Hauer, 1856 — *Cenoceras*
N. subalbensis Sinzow, 1913 — *Anglonautilus*
N. subbiangulatus d'Orbigny, 1850 — *Pseudaganides*
N. subfleuriausianus d'Archiac, 1850 — *Angulithes*
N. (Paracenoceras) subhexagonus Jeannet, 1951 — *Paracenoceras*
Eutrephoceras subinflatus d'Orbigny, 1850 — *Eutrephoceras*
N. sublaevigatus d'Orbigny, 1840 — *Eutrephoceras*
N. subplicatus Philippi (*in* Sleinmann, 1895) — *Eutrephoceras*
Cimomia subrecta Miller and Thompson, 1933 — *Cimomia*
N. subrotundus Crick, 1898 — *Cenoceras*
N. subsinuatus d'Orbigny, 1850 — *Pseudaganides*
N. subtruncatus Morris and Lycett, 1850 — *Procymatoceras*
N. subtruncatus Prinz, 1906 — *Cenoceras*
N. suciensc Whiteaves, 1879 — *Cymatoceras*
Cimomia sudanensis Miller, 1951 — *Cimomia*
N. szontaghi Vogl, 1910 — *Eutrephoceras*
N. tamulicus Kossmat, 1897 — *Angulithes*
N. tennicostatus Schlüter, 1876 — *Cymatoceras*
N. terebratus Dumortier, 1874 — *Cenoceras*
Cimomia tessieri Miller, 1951 — *Cimomia*
N. texanum Shumard, 1860 — *Paracymatoceras*
Eutrephoceras thomi Reeside, 1927 — *Eutrephoceras*
N. thyrrenus Tagliarini, 1901 — *Cenoceras*
N. toarcensis d'Orbigny, 1849 — *Cenoceras*
Deltoidonautilus togoensis Miller, 1951 — *Angulithes*
Aturia tokunagai Shimizu, 1926 — *Aturia*

N. tourtiae Schlüter, 1876 — *Cymatoceras*
Aturia (Brazaturia) triangulata Stenzel, 1935 — *Aturia*
N. triangularis Montfort, 1802 — *Angulithes*
N. tricarinatus Vadász, 1911 — *Cenoceras*
N. trichinopolitensis Blanford, 1861 — *Paracymatoceras*
N. truncatus J. Sowerby, 1816 — *Cenoceras*
N. tskaltsithelensis Rouchadzé, 1931 — *Cymatoceras*
Neocymatoceras tsukushiense Kobayashi, 1954 — *Cymatoceras*
N. tubingensis Loesch, 1914 — *Pseudaganides*
N. tumescens Frauscher, 1895 — *Eutrephoceras*
Hercoglossa tuomeyi Clark and Martin, 1901 — *Hercoglossa*
N. turcicus Krumbeck, 1905 — *Cimomia*
N. turkeryi Gemmellaro, 1886 — *Pseudaganides*
Aturia (Brazaturia) turneri Stenzel, 1940 — *Aturia*
Platynautilus tyôsiensis Yabe and Ozaki, 1953 — *Heminautilus*
Eutrephoceras uitenhagense Spath, 1930 — *Eutrephoceras*
Enclimatoceras ulrichi White, 1882 — *Hercoglossa*
N. umbilicaris Deshayes, 1835 — *Eutrephoceras*
Cymatoceras undulatiformis Spath, 1927 — *Cymatoceras*
N. undulatus J. Sowerby, 1813 — *Anglonautilus*
N. urbanus J. de C. Sowerby, 1843 — *Eutrephoceras*
N. vaalsensis Binckhorst, 1861 — *Epicymatoceras*
Nautilopsis vanuxemi Conrad, 1847 — *Aturia*
N. vastus Kner, 1850 — *Eutrephoceras*
N. vaughani Gardner, 1923 — *Cimomia*
N. ventroplicatus Foord, 1891 — *Cymatoceras*
Cimomia vestali Miller and Thompson, 1933 — *Cimomia*
N. vicentinus Oppenheim, 1901 — *Eutrephoceras*
N. victorianus Teichert, 1943 — *Eutrephoceras*
Aturoidea vicirai Miller, 1951 — *Aturoidea*
N. vinassai Venzo, 1937 — *Eutrephoceras*
N. (Cymatoceras) virgatus Spengler, 1910 — *Cymatoceras*
N. volgensis Nikitin, 1888 — *Paracenoceras*
N. waageni Gemmellaro, 1886 — *Cenoceras*
Hercoglossa walteri Miller, 1947 — *Hercoglossa*
N. wandaense Waagen, 1873 — *Paracenoceras*
Hercoglossa waringi Miller, 1947 — *Hercoglossa*
N. westphalicus Schlüter, 1872 — *Angulithes*
N. (Paracenoceras) wilmae Jeannet 1951 — *Paracenoceras*
N. woodsi v. Hoepen, 1921 — *Cymatoceras*
N. wyllei Newton, 1925 — *Cimomia*
Aturia yokoyamai Nagao, 1926 — *Aturia*
N. ziczac J. Sowerby, 1812 — *Aturia*
N. zignoi Gemmellaro, 1886 — *Cenoceras*

N. zitteli Gemmellaro, 1886 — *Cenoceras*
Tithonoceras zitteli Retowski, 1894 — *Tithonoceras*

The following are species for which the available data is insufficient to place them in a generic group with any degree of certainty.

N. astierianus d'Orbigny, 1850
N. delphinus Forbes, 1846
N. fricator Beck, 1835 (nomen nudum)
N. hartmanni Loesch, 1914 (nomen nudum)
N. herbertinus d'Orbigny, 1850
N. inaequalis J. Sowerby, 1813
N. krenkeli Loesch, 1914 (nomen nudum)
N. marcoui d'Orbigny, 1850
N. matheronianus d'Orbigny, 1841
N. naufragus Craigin, 1905
N. nobilis Münster (see Foord, 1891, p. 326) (nomen nudum)
N. normannicus Loesch, 1914 (nomen nudum)
N. pseudoganiticus Loesch, 1914 (nomen nudum)
N. reussii Fritsch and Schlönbach, 1872
N. staffelbergensis Loesch, 1914 (nomen nudum)
N. sumatranus Zwierzycki, 1915
N. tenuiplanatus Dana, 1849
N. valenciennii Hupé (*in* Gay, 1854)
N. varusensis d'Orbigny, 1850
N. wepferi Loesch, 1914 (nomen nudum)

EVOLUTION

Evolutionary patterns, characterized by almost complete extinction followed by adaptive phases with both eruptive and stable periods, are well displayed in the general history of the Cephalopoda. Few other invertebrate groups display such marked expansion and contraction in their evolution. Within the ammonoids, periods of abrupt contraction, characterized by mass extinction of most evolving lines, occurred in the late Permian and in the late Triassic. Complete extinction of the group came at the end of the Cretaceous. Within the ammonoids each of the two earlier periods of near extinction was followed by an even greater evolutionary radiation. This is well illustrated by the number of genera involved in each of these phases: there are 172 genera of ammonoids of Devonian to Permian age, 370 in the Triassic, and 1228 in the Jurassic and Cretaceous.

There is some parallelism to the ammonoid history in the evolution of the nautiloids; however, in the latter group instead

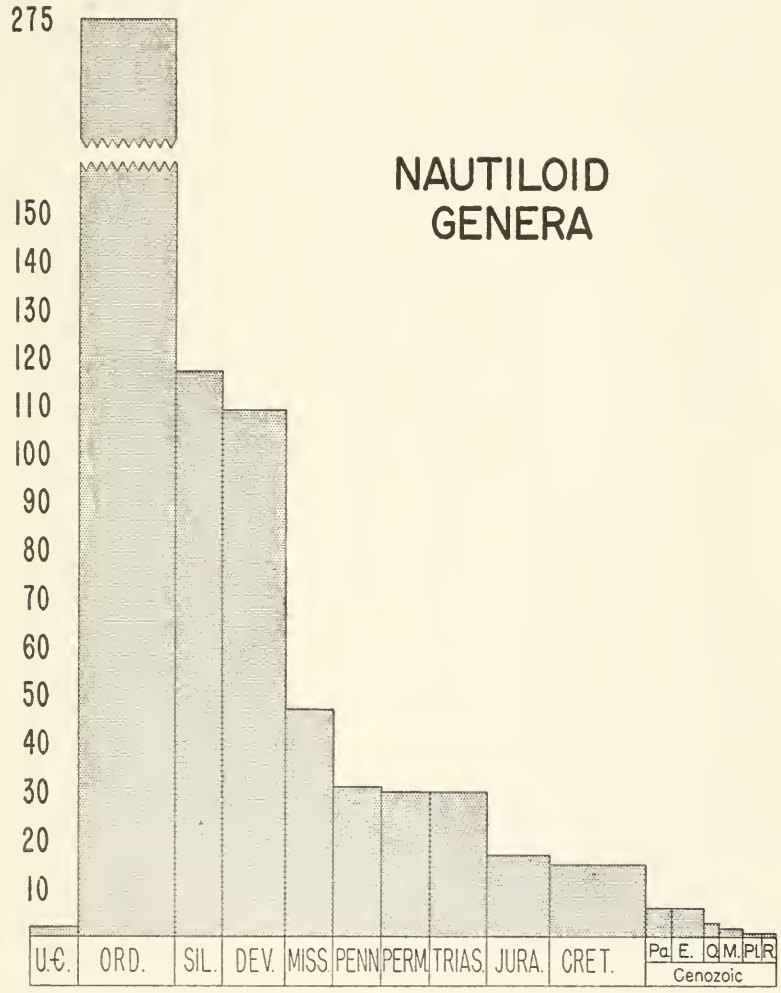

Fig. 1. Bar chart showing number of genera of nautiloid cephalopods present in each period.

of an ever expanding evolutionary complex, the nautiloids experienced their widest radiation in the Ordovician relatively soon after their appearance in the Upper Cambrian. Soon after this period of maximum expansion, there set in a steady, gradual contraction in numbers and diversity of taxonomic units (Fig. 1). There is no wave of extinction toward the end of the Paleozoic; in fact the whole evolutionary pattern of Triassic nautiloids is really a culmination of trends begun back in the Carboniferous (Kummel, 1953c). Thus the evolutionary phases at the transition from the Paleozoic to the Mesozoic are quite different in the ammonoids and the nautiloids. However, toward the end of the Triassic most of the long-persisting Carboniferous to Triassic stocks became extinct. This phase of the evolutionary history of the nautiloids has recently been discussed by Kummel (1953c). There are, in fact, no Rhaetic nautiloids known.

The earliest marine deposits of the Jurassic contain a very homogeneous nautiloid fauna of nearly world-wide distribution. Insofar as nautiloids are concerned, there must have existed at the transition period from the Triassic to the Jurassic an ecologic vacuum. A single stock survived this transition period from the Triassic (Kummel, 1953b), and in the early Jurassic (Lias) an intensified and new evolutionary radiation took place (Fig. 2). The early Jurassic stocks are quite clearly of a single genetic complex, but at the same time show a wide adaptive range in terms of conch shape, size, suture, and shell characters. All these features reflect and express the wide adaptive radiation that took place at this time. Whereas there is very little factual data available as to the adaptive significance of most morphological features it seems only logical to conclude that the various conch shapes, etc., represent adaptations to a specific niche in the marine environment. The repopulation of the early Jurassic seas by nautiloids was uninhibited as far as other nautiloid groups are concerned, and the diversity of conch types is cogent testimony to the adaptation to and occupation of many environmental niches.

Eruptive phases expressed in terms of great plasticity of a group are quite common among the ammonoids. Spath (1934, p. 19) has drawn attention to the "sudden burst of Gephuroceratids in the Upper Devonian of the Domanik, Southern Timan. In that locality there appeared in large numbers depressed and

compressed, smooth and ornamented, evolute and involute, rounded, square, or acute-ventered forms, and even highly

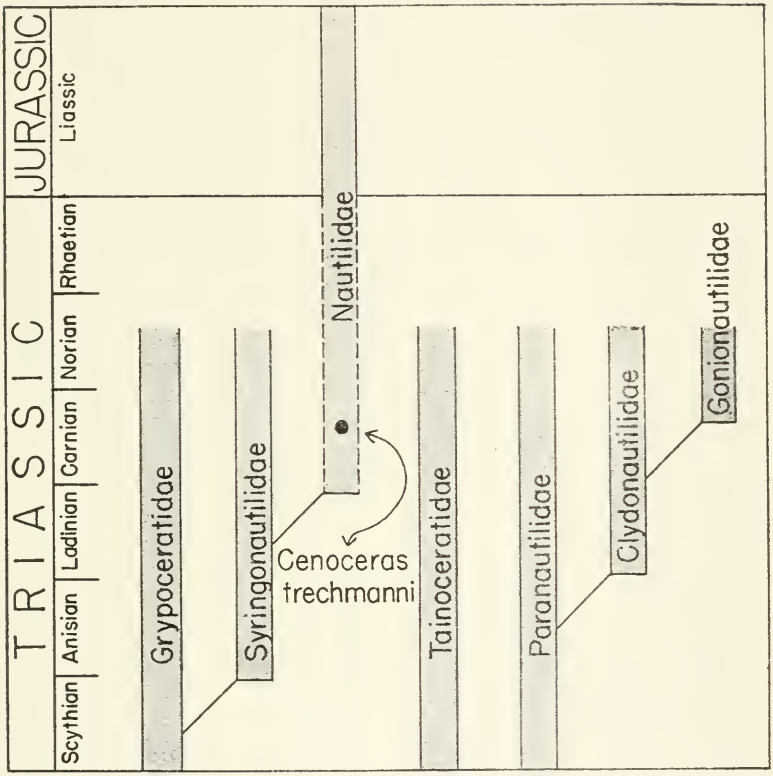

Fig. 2. Phylogenetic diagram illustrating the relationships of the Liassic Nautilidae with the Triassic nautiloid families. The columns representing the Triassic families have been terminated at an arbitrary even line in the Norian. The exact relative extinction dates of these families in the Norian are not known.

specialized oxycones" (See Holzapfel, 1899). A similar situation is found with the early Triassic ophiceratids of the Himalayas (Diener, 1897) and Greenland (Spath, 1930a, 1935a). More examples can be found within the Jurassic and Cretaceous ammonoids.

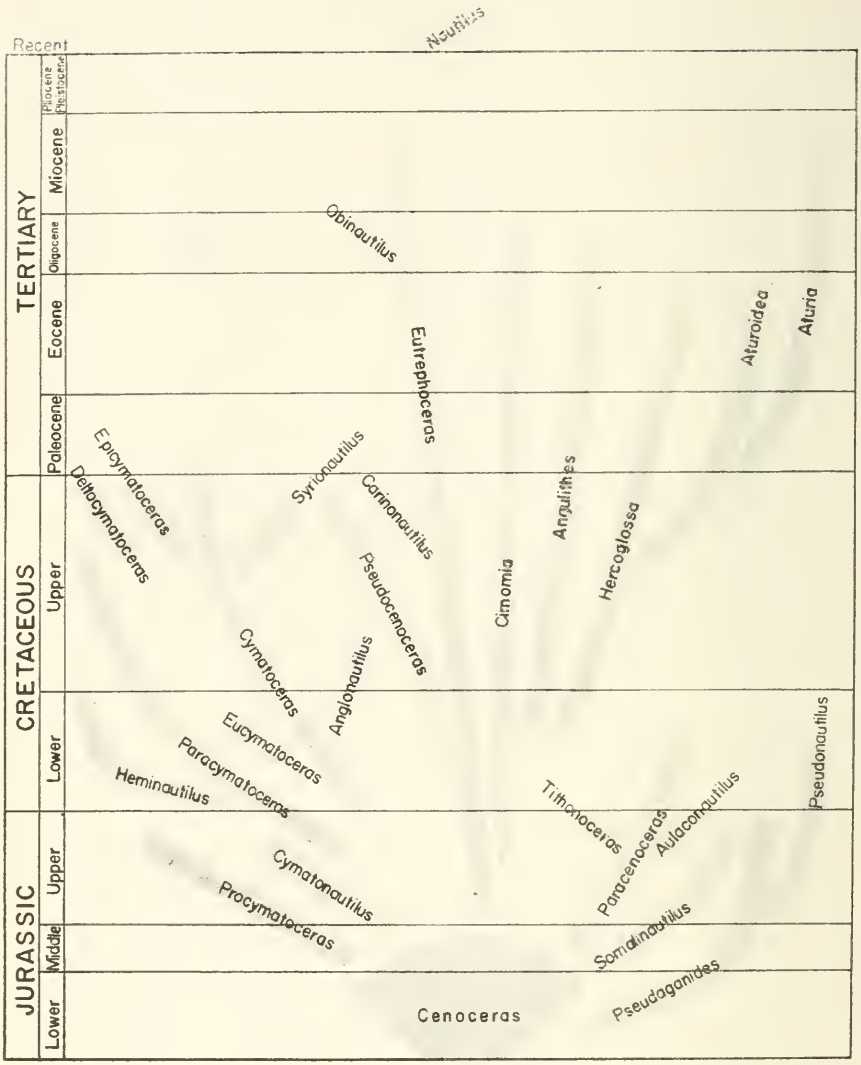

Fig. 3. Diagram showing inferred phylogeny and geologic distribution of post-Triassic nautiloids.

Most early Jurassic nautiloids are here considered species of a single genus, *Cenoceras*. The earliest species of *Cenoceras*, *C. trechmanni*, is from Carnian strata of New Zealand and is derived from the Syringonautilidae (Kummel, 1953b). No species of any other Triassic stock survived into the Jurassic. In the Lias there is thus a world-wide fauna of involute to evolute, strigate to smooth forms with a wide range in whorl shapes — a genetic complex of great plasticity. From this homogeneous but plastic stock there arose from diverse parts of the complex several distinct evolutionary lines built on specialization of one or more morphological features. From this *Cenoceras* complex arose the persisting stable stock (*Eutrephoceras*) which gave rise to other members of the Nautilinae. Likewise the Pseudaganidinae, Paracenoceratinae and most probably the Cymatoceratinae arose directly out of the *Cenoceras* complex (Fig. 3).

The Pseudaganidinae are characterized by their sinuous sutures. In this respect they are adaptive types like the Triassic Clydonautilidae, Gonionautilidae, and Siberionautilidae. They are likewise similar to these Triassic groups in that they show stability in the general form and patterns of the suture and great variability in conch shape. The Pseudaganidinae range from the Liassic into the Lower Cretaceous. There are only two genera involved in this radiation, of which *Pseudaganides* is the main line and *Pseudonautilus* is a specialized offshoot of Upper Jurassic and Lower Cretaceous age. In the evolutionary history of the nautiloids from the Carboniferous to the Recent, adaptive trends expressed in terms of sinuous — "goniatitic" — sutures occurred at four separate times. The first is known through the genus *Permoceras* Miller and Collinson based on *Aganides bitauniense* Haniel from Middle Permian strata of Timor. In my opinion, *Permoceras* is related to the *Grypoceras-Domatoceras* evolving stock and is an aberrant development of this stock. *Grypoceras* (*Plummeroceras*) Kummel (1953c) likewise had a highly sinuous suture with a deep ventral lobe and a deep lateral lobe but it has a very evolute conch. The second radiation repeating this adaptive trend is that in the Upper Triassic including the Clydonautilidae, Gonionautilidae and Siberionautilidae. All of the genera of these families include species with very involute conchs but show great variability in conch shape. The

only other Triassic species with a "goniatitic" suture is *Clymenonautilus ehrlichi* Mojsisovics which in all features but the suture is allied to the Syringonautilidae. The suture however has a deep, tongue-shaped, narrow, lateral lobe. The Upper Triassic families listed above which include those involute species with highly sinuous sutures, evolved from involute, smooth forms with nearly straight sutures (Paranautilidae).

The third radiation of this series is that of the Pseudaganidinae of Lower Jurassic to Lower Cretaceous age. This group evolved out of some part of the *Cenoceras* complex in the Lias. There is almost perfect homeomorphy between *Permoceras bitauniense* Haniel of the Middle Permian and *Pseudonautilus geinitzi* Oppel of the Upper Jurassic (Miller and Collinson, 1953). Each however represents similar adaptive types from different root stocks and they are not related.

The fourth and last radiation centered on the sinuosity of the suture is that of the Hercoglossinae and Aturinae. The Aturinae with its single genus *Aturia* is a very specialized development out of the Hercoglossinae. The specialization in this case is not so much on a further elaboration of the suture but in the development of the peculiar dorsal siphuncle. Within the Hercoglossinae there is a beautiful developmental series (usually treated as genera) showing gradual increase in sutural complexity. The subfamily has its origin within the stable evolving stock of the Nautilinae represented by *Eutrephoceras* which is characterized by an involute smooth conch with straight or slightly sinuous sutures. *Cimomia* of the Hercoglossinae has a slightly more individualized suture and is gradational with *Eutrephoceras*, as it is also with *Hercoglossa* which has very distinct lobes and saddles. *Angulithes* is merely a sagittate development of these forms. In *Aturoidea* the sutural individuality is carried slightly farther.

The Paracenoceratinae is a small subfamily of mainly Jurassic age with four genera characterized by specialization of the venter. The main stock of this subfamily, *Paracenoceras*, is nearly worldwide in distribution and has by far the largest number of species. The other genera, namely *Somalinautilus*, *Aulaconautilus*, and *Tithonoceras* are more highly specialized forms with few known species. In *Paracenoceras* the whorl section is subtrapezoid, generally with a broad, sulcate venter. *Somalinautilus* has angu-

lar ventral shoulders but a broad arched venter. *Aulaconautilus* has four or more longitudinal ribs. In this respect it is homeomorphous to *Aulametacoceras* of the Permian and Triassic. *Tithonoceras* has prominent rounded ventrolateral keels with a sulcate venter. *Paracenoceras* and *Somalinautilus* are undoubtedly derived from distinct elements of the *Cenoceras* complex but *Aulaconautilus* and *Tithonoceras* appear to be specialized developments of *Paracenoceras*.

One of the most successful and diverse groups to stem directly or indirectly from the *Cenoceras* complex is the Cymatoceratinae. This subfamily comprising 10 genera ranging from the Jurassic to the mid-Tertiary is characterized by conchs bearing ribs. This is the only group of post-Triassic nautiloids to have ornamentation, aside from *Aulaconautilus* of the Paracenoceratinae. Radiation within the Cymatoceratinae is reflected in the shape of the conch, suture and ornamentation. The main evolving stock, *Cymatoceras*, has an involute, rounded conch with only a slightly sinuous suture. Most of the other genera of this subfamily are thought to represent various specialized groups derived from *Cymatoceras*. *Paracymatoceras* has a more sinuous suture, in fact much like that of *Hercoglossa*, and on even this feature it is gradational with *Cymatoceras*. Those forms differentiated on the basis of conch shape include *Heminautilus*, *Deltocymatoceras* (n. gen. p. 438), *Epicymatoceras* (n. gen. p. 439) and *Cymatonautilus*. *Herminautilus* has a compressed involute conch with a highly sinuous suture, that has deep ventral and lateral lobes. *Deltocymatoceras* is a homeomorph of *Angulithes* with a sagittate whorl section. *Epicymatoceras* has an evolute, highly compressed conch with a subrectangular whorl section. *Cymatonautilus* has a concave venter and concave lateral areas. Those genera differentiated on the basis of modification of the ribbing pattern include *Eucymatoceras*, *Anglonautilus*, *Procymatoceras*, and *Syrionautilus*. In *Eucymatoceras* the ribs form prominent V-shaped salients on the venter and flanks. In *Anglonautilus* there are coarse folds on the venter whereas *Procymatoceras* has a rapidly expanding robust conch with ribs mainly on the lateral areas. *Syrionautilus* has peculiar shaped ribs with wide interspaces like that of *Proclydonautilus spirolobus* of the Triassic. *Cymatonautilus* and *Procymatoceras* are Jurassic developments, the remaining genera mostly Cre-

taceous. In fact the most widespread and characteristic nautiloids of the Cretaceous are genera of the Cymatoceratinae.

Thinking of the Cymatoceratinae as representing a single genetic unit with its origin within the *Cenoceras* complex, and having as the basic common denominator the ribbing pattern, all of the diverse morphologic types represented by the various genera reflect a broad adaptive radiation which produced numerous homeomorphs of other genera of the Nautilidae.

The most persistent stock evolved from the early Jurassic *Cenoceras* complex is that of *Eutrephoceras*. This genus has a world-wide distribution and ranges in time from the Upper Jurassic to mid-Tertiary. It and *Cymatoceras* are the most common post-Triassic nautiloids. Some 90 so-called species, assigned to this genus, have been described. The genotype has a tightly involute, subglobular, smooth conch with a nearly straight suture. This basic, very simplified, conch pattern became modified either by greater compression, depression or by slightly looser coiling. The variants, however, on the basis of the record available appear to be completely random in their chronologic or geographic distribution. Each such variant has usually been treated as a distinct species. The geologic record thus shows the occurrence of nautiloids with the basic, simplified, globose conch persisting from Upper Jurassic to mid-Tertiary time and with numerous variants of this basic pattern.

Whereas the suture is generally straight or nearly so there are gradational forms to *Cimomia*. Data are not available as to whether there is any particular chronologic or geographic relationship in regard to the sutural variants, which appear to be completely random as is the case with conch form.

The eutrephoceratids are thus a persisting generalized stock which arose from the *Cenoceras* complex, and they show no particular adaptive trends throughout their history. They do show, however, a certain variability in conch shape and suture. The group has the longest range of any of the post-Triassic nautiloids. It is from this persisting generalized form that the remaining more specialized genera and subfamilies arose. The most important offshoots are the genus *Nautilus* and the whole subfamily Hercoglossinae. The nature of the evolutionary pattern from *Eutrephoceras* to *Cimomia* is not easy to decipher. The only significant difference is the degree of sinuosity of the

suture, that in *Eutrephoceras* being straight, or nearly so, and that in *Cimomia* having a distinct lobe and saddle on the lateral areas. There are gradational forms between these two genera. The time range of the two genera is approximately the same, *Cimomia* being slightly younger in origin. It seems quite clear that *Cimomia* arose from *Eutrephoceras* but whether or not there was a single time and point of origin in the late Jurassic, or if

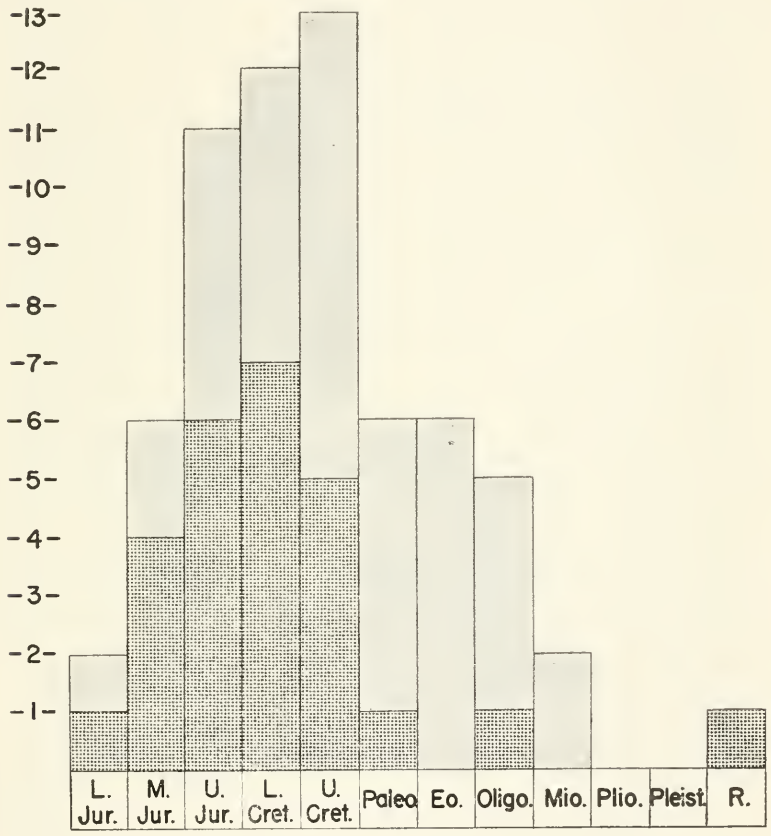

Fig. 4. Bar chart showing total number of genera of nautiloids present in each series of the Mesozoic and Tertiary (light stippling) and number of new genera appearing for the first time in each series (dense stippling).

there were numerous times of origin, throughout the Cretaceous and Tertiary cannot be told from the kind of data available. The alternatives are a parallel evolutionary pattern of the two genera or a consideration of these transitional forms of suture (*Cimomia*) as a form genus including numerous distinct radiations from the eutrephoceratid evolving stock.

Iterative patterns of evolution are recognized within the Carboniferous through Triassic nautiloids. With these nautiloids three main, slowly-evolving, persisting stocks are recognized, namely the *Domatoceras-Grypoceras* line, the *Metacoceras-Mojsvaroceras* line, and the *Liroceras-Paranautilus* line. Each of these stocks has a relatively large number of species (which is merely an indication of relative abundance) and is widespread geographically. Throughout their history they show only relatively minor evolutionary changes. Each of these lines represents a stable, slowly-evolving, but persisting parent stock of their particular family groups. These lines are the evolutionary reservoirs from which other, generally more specialized, groups evolved. The offshoots most often are adaptations accentuating one or more generalized characters of the parent stock. Most of the offshoots are forms with few species and limited geographic range. However, some of these offshoots became in themselves virile, evolving stocks, each with a wide adaptive range and many species (e.g. Pleuronautilidae from the *Metacoceras-Mojsvaroceras* line and the Clydonautilidae from the *Liroceras-Paranautilus* line).

The *Eutrephoceras* stock gave rise to four other small and aberrant groups, *Pseudocenoceras*, *Obinautilus*, *Carinonautilus*, and *Nautilus*. *Pseudocenoceras* is a compressed form somewhat evolute and with an arched venter, flattened sides and steep umbilical shoulders. *Carinonautilus* is a much compressed form with a prominent rounded keel. It is a monotypic form from Upper Cretaceous strata of South India. *Obinautilus* is another monotypic form recently described by Kobayashi from Oligocene strata of Japan. It is a much compressed involute form with a shallow but distinct furrow on the venter. This genus is still very incompletely known since on the type and only available specimen neither the suture nor position of the siphuncle is preserved.

No fossil species are assigned to the genus *Nautilus*. No Plio-

cene or Pleistocene nautiloids are known. Several species of Eocene, Oligocene, and Miocene age have been at times assigned to *Nautilus* but all of these are here considered as having closer affinities to the persisting eutrephoceratid stock than to modern species of *Nautilus*.

TABLE 1

	L. Jur.	M. Jur.	U. Jur.	L. Cret.	U. Cret.	Paleoc.	Eocene	Oligo.	Mio.	Plio.	Recent
Cenoceras	x	x									
Eutrephoceras			x	x	x	x	x	x	x		
Pseudocenoceras				x	x						
Carinonautilus					x						
Obinautilus								x			
Nautilus											x
Pseudaganides	x	x	x								
Pseudonautilus			x	x							
Paracenoceras		x	x	x							
Aulaconautilus			x								
Tithonoceras			x								
Somalinautilus		x	x								
Cymatoceras				x	x			x			
Paracymatoceras			x	x	x						
Procymatoceras		x	x								
Cymatonautilus		x	x								
Anglonautilus				x	x						
Eucymatoceras				x							
Syrionautilus					x						
Heminautilus				x							
Deltocymatoceras					x						
Epicymatoceras					x						
Cimomia			x	x	x	x	x	x			
Angulithes				x	x	x	x	x			
Hercoglossa				x	x	x	x				
Aturoidea					x	x	x				
Aturia						x	x	x	x		

The geologic range of the genera of post-Triassic nautiloids is summarized on Table 1, and the bar chart of Figure 4 shows the number of genera and number of new genera per series division of the Jurassic, Cretaceous, and Tertiary. This bar chart clearly brings out the increasing adaptive diversity of the nautiloids in their resurgence after their near extinction in the late Triassic. There is a gradual increase in numbers of new types through the Jurassic. However, of the total of 11 genera in the Upper Jurassic, only 3 (*Eutrephoceras, Paracymatoceras* and *Cimomia*) are still destined for a long history. More than half of the total Upper Jurassic fauna (6 genera) do not survive into the Cretaceous and 2 genera (*Pseudonautilus* and *Paracenoceras*) have their main evolutionary play in the Upper Jurassic with only a few species known from Lower Cretaceous. Thus the Jurassic faunas are replaced in the Cretaceous by new phyletic lines, mainly of the Cymatoceratinae, with a much smaller portion from the Nautilinae and Hercoglossinae. By the early Tertiary the cymatoceratid radiation is almost at an end, with a single surviving species in the middle Tertiary. Only one new genetic unit, the Aturinae, comes into the picture in the Paleocene; this became by mid-Tertiary time the most conspicuous element of the fauna. Early Tertiary time was the heyday of the Hercoglossinae; however, the origin of all members of this radiation is well down in the Cretaceous. Wherever early Tertiary faunas are found, members of the Hercoglossinae are the principal elements; the great number of species of this subfamily for the early Tertiary merely reflects the large amount of study concentrated on them in recent years, especially by Miller.

Thus from this summary picture, post-Triassic nautiloid evolution took place in three successive waves, one in the Jurassic, another in the Cretaceous, and the last in the early Tertiary. Each wave introduced new genetic lines which gradually replaced existing or previous lines. The Jurassic and Cretaceous radiations are of approximately equal magnitude; that of the early Tertiary is greatly reduced. Whether or not *Nautilus* should be considered an additional radiation is a moot question. Of the derivations from the eutrephoceratid surviving stock only the Hercoglossinae had an extensive evolutionary history. The other offshoots including *Nautilus* are either monotypic or represented by few species of no great geographic or stratigraphic

range. It seems highly likely that *Nautilus* will follow this same fate.

In most of the principal evolutionary trends of the post-Triassic nautiloids the main evolving stock of each subfamily is repre-

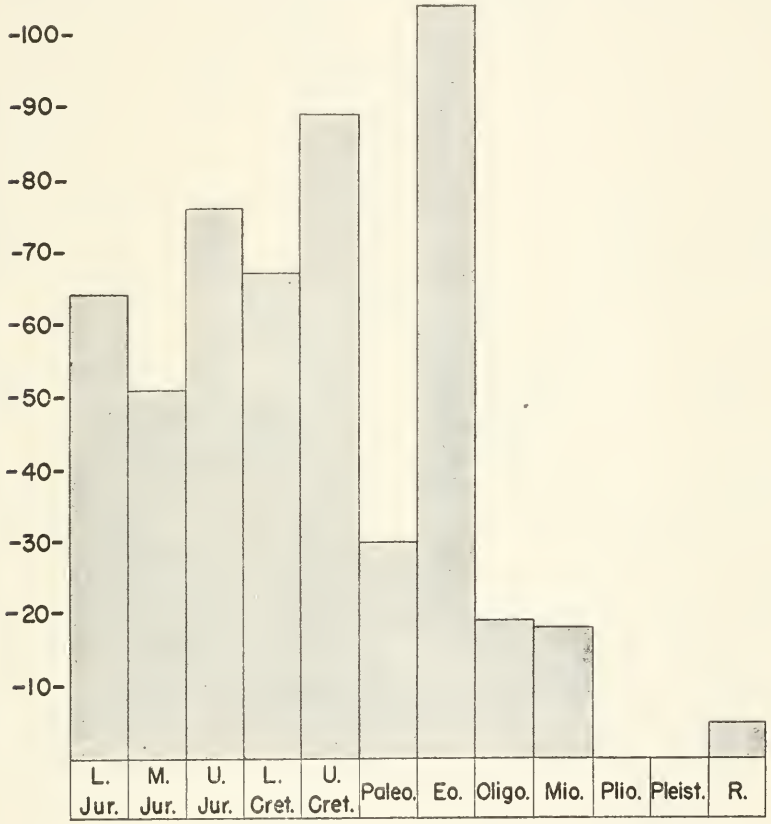

Fig. 5. Bar chart showing total number of species of nautiloids for each series of Mesozoic and Tertiary.

sented by the largest number of species, with the other genera having only a fraction of that amount. Thus of the Nautilinae, *Cenoceras* and *Eutrephoceras* have by far the largest number of species. In the Paracenoceratinae, it is *Paracenoceras;* in the

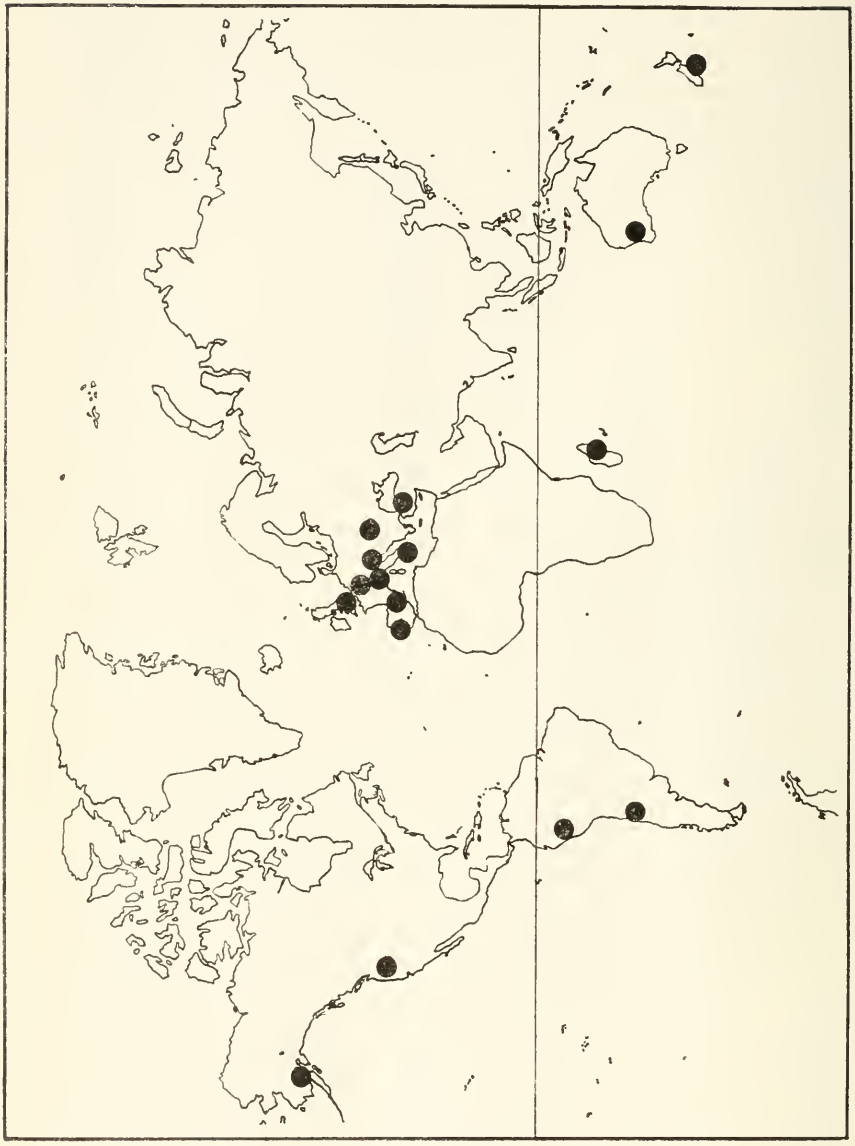

Fig. 6. Geographic distribution of species of the genus *Cenoceras* in formations of Lower and Middle Jurassic age.

Fig. 7. Geographic distribution of species of the genus *Eutrephoceras* in formations of Upper Jurassic, Cretaceous, and Tertiary age. Circles = Tertiary; left half circles = Cretaceous; right half circles = Jurassic.

Cymatoceratinae, it is *Cymatoceras;* in the Pseudaganidinae it is *Pseudaganides*, and in the Hercoglossinae it is *Cimomia* that has the greatest number of species. The Aturinae has only the genus *Aturia*. In spite of the unsatisfactory nature of our understanding of most nautiloid species, these named units do express morphologic diversity, geographic range, and general abundance in nautiloid faunas of these periods. These data likewise tend to substantiate the thesis presented here for persisting, evolving stocks of wide geographic distribution from which more restricted adapted types evolved. On Figure 5 are summarized the number of species per series of the Jurassic, Cretaceous, and Tertiary. Except for the large number of early Tertiary species, interpreted here as a monographic high, this bar chart reflects very well the bar chart on distribution of genera during this time span.

SYSTEMATIC PALEONTOLOGY

Family NAUTILIDAE d'Orbigny, 1840

This family is interpreted here to include all post-Triassic nautiloid genera, which are placed in six subfamilies: Nautilinae d'Orbigny, Pseudaganidinae nov., Paracenoceratinae Spath, Cymatoceratinae Spath, Hercoglossinae Spath, and Aturinae Hyatt. The overall evolutionary pattern of post-Triassic nautiloids with the plastic *Cenoceras* complex of the early Jurassic from which developed directly or indirectly several distinct phyletic trends produced a very homogeneous evolutionary unit. The subfamily units are adaptive trends interpreted for the most part on the basis of single characters — in the Cymatoceratinae it is the presence of ribbing; in the Paracenoceratinae it is elaboration of the periphery; in the Hercoglossinae and Pseudaganidinae it is elaboration of the suture; and in the Aturinae it is the unique dorsal siphuncle and its structure. None of these trends is really a major shift in the evolutionary complex but each is more in the nature of elaboration of genetic potentials in the evolving parent stocks. It thus seems that the taxonomic ranks used here reflect the phylogenetic picture.

Subfamily NAUTILINAE d'Orbigny, 1840

The Nautilinae includes among its genera the earliest forms and the latest and living species of the Nautilidae. Thus in the history of this subfamily we have the origin of the Nautilidae, the persisting stock which gave rise to the remaining subfamily units, and the few living species represented by the relic genus *Nautilus*. The genera included in the Nautilinae are: *Nautilus*, *Cenoceras*, *Eutrephoceras*, *Pseudocenoceras*, *Carinonautilus*, and *Obinautilus*. *Cenoceras* is the plastic evolving complex which survived the great period of extinction at the end of the Triassic and experienced a very intense radiation in the early Jurassic. From the *Cenoceras* complex arose the Pseudaganidinae, Paracenoceratinae, and probably the Cymatoceratinae. *Eutrephoceras* is interpreted as a slowly evolving, long persisting, generalized stock also derived from the *Cenoceras* complex and from which the remaining members of the Nautilinae were derived plus the Hercoglossinae.

Carinonautilus and *Obinautilus* are monotypic; *Pseudocenoceras* has 8 species, and *Nautilus* only 5 species (all Recent). However, *Cenoceras* has 97 species and *Eutrephoceras* 90. This great number of species (or named units) reflects the wide geographic range, morphologic diversity and relative abundance of these two genera. *Cenoceras* is mainly confined to the Lower and Middle Jurassic (with one Upper Triassic [Carnian] species), and *Eutrephoceras* ranges from the Upper Jurassic into the Miocene. Both genera have world-wide distributions (Figs. 6, 7).

Genus CENOCERAS Hyatt, 1883

Cenoceras Hyatt, 1883, pp. 300 301.
Cenoceras Hyatt, 1894, p. 550.
Digonioceras Hyatt, 1894, pp. 548-549.
Nautilites Prinz, 1906, p. 201.
Cenoceras Spath, 1927a, pp. 20 24.
Ophionautilus Spath, 1927a, pp. 21, 24.
Sphaeronautilus Spath, 1927a, pp. 21, 24.
Cenoceras Flower and Kummel, 1950, p. 615.
Bisiphytes (Cenoceras) Kummel, 1954, p. 322.
Type species. *Nautilus intermedius* d'Orbigny non Sowerby=*N. orbignyi* Prinz (1906, p. 213). By original designation. Type illustration reproduced on Plate 1, figs. 1, 2.

The genus *Cenoceras* is here interpreted to include those nautiloid species of the Liassic and Inferior Oolite that are part of the evolving complex which survived the Triassic and which in the great plasticity of the group reflect an extensive adaptive radiation. It is from this very plastic adaptive unit that the more stable, more clearly defined evolutionary lines evolved. The nautiloids nearly became extinct at the end of the Triassic. A single surviving line derived from the Syringonautilidae gave rise to the sole surviving stock (Spath, 1927a, p. 23; Kummel, 1953b). This surviving stock entered an environmental vacuum (insofar as nautiloids are concerned) in the earliest Jurassic. The re-occupation of the diverse ecological niches available for a homogeneous unit stock gave rise to many morphological types, especially in regard to conch form. It is not possible at this time to decipher the individual evolutionary lines within the main complex. There is a complete range of variation and gradation in conch form, suture, position of siphuncle, ornamentation, etc. To bring the taxonomy of these nautiloids to reflect the phylogenetic interpretation, all of the genera previously proposed for aberrant types in the Liassic are placed in synonymy of *Cenoceras*. There is no particular reason for retaining these genera since their included species fit well within the range of variability and evolutionary pattern of the genus *Cenoceras*.

Fig. 8. Cross sections of the conch of species of *Cenoceras*. Redrawn from Pia (1914, pl. 8 [5]). *A*, *C. araris* (Dumortier) after Dumortier, diameter 210 mm.; *B*, *C. arariformis* (Pia) after Pia, diameter 190 mm.; *C*, *C. adneticus* (Pia) after Pia, diameter 137 mm.; *D*, *C. domeykus* (d'Orbigny) after d'Orbigny, diameter 150 mm.; *E*, *C. stoppani* (Parona) after Parona, diameter 142 mm.; *F*, *C. baconicus* (Vadász) after Vadász, diameter 50 mm.; *G*, *C. altisiphites* (Prinz) after Prinz, diameter 60 mm.; *H*, *C. julianus* (Fucini) after Fucini, diameter 20 mm.; *I*, *C. simillimus* (Foord and Crick) after Pia, diameter 107 mm.; *J*, *C. secernendus* (Pia) after Pia, diameter 135 mm.; *K*, *C. ornatus* (Foord and Crick) var. *atanatensis* (Pia) after Pia, diameter 158 mm.; *L*, *C. paretoi* (Gemmellaro) after M. Gemmellaro, diameter 17.5 mm.; *M*, *C.* sp. ind. No. 2, after Prinz, diameter 65 mm.; *N*, *C. striatus* (Sowerby) after d'Orbigny, diameter 110 mm.; *O*, *C. striatus* (Sowerby) after Hauer, diameter 80 mm.; *P*, *C. sturi* (Hauer) after Hauer, diameter 65 mm.; *Q*, *C. semseyi* (Prinz) after Prinz, diameter 88 mm.; *R*, *C. robustus* (Foord and Crick) after Foord, diameter 200 mm.; *S*, *C. geyeri* (Prinz) after Geyer, diameter 80 mm.; *T*, *C. fourneti* (Dumortier) after Dumortier and Pia, diameter 80 mm.

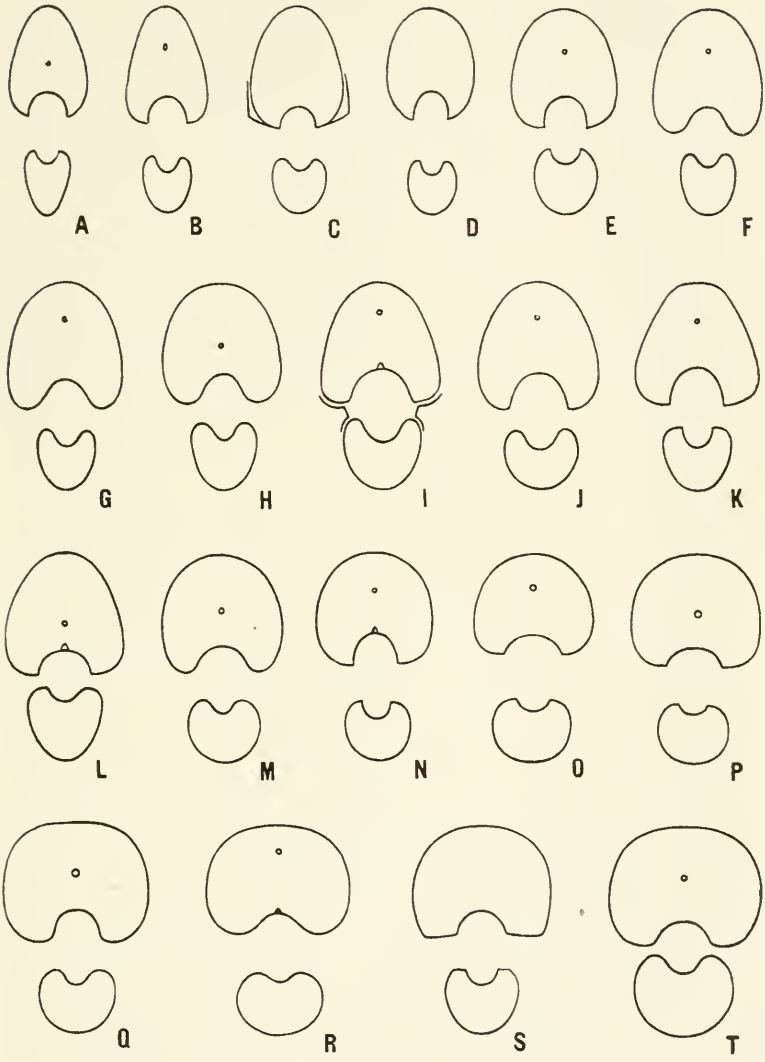

Figure 8

Nomenclature of early Jurassic nautiloids has an involved and ambiguous history. As pointed out by Spath (1927a, p. 20), Hyatt's genus *Cenoceras* (for the group of *Nautilus intermedius* d'Orbigny non Sowerby) has been universally rejected, since Hyatt left in *Nautilus s.s.* other members of the same group, such as *Nautilus striatus*. However, Spath in his 1927 revision of post-Triassic nautiloids accepted *Cenoceras* as a distinct unit on the basis of Hyatt's (1894, p. 550) revised definition limiting *Cenoceras* to forms with a trigonal ananepionic, a subquadragonal metanepionic, and a dorsally sulcate nepionic stage. At the same time Spath readily recognized that the groups of *Nautilus striatus* Sowerby and *Nautilus intermedius* Sowerby could not be differentiated on the shape of the conch and they "agree in ornamentation, position of the siphuncle, presence of an annular lobe, and chiefly in the course of the septal suture" (Spath, 1927a, p. 20).

Now for the group of *Nautilus striatus* Sowerby, Spath revived the genus *Bisiphytes* Montfort (1808). This genus has been discussed to a varied degree by Spath (1927a, pp. 19-24), Miller, Dunbar, and Condra (1933, pp. 42, 43), Teichert (1940, p. 591) and Kummel (1954, pp. 322-323). Montfort listed as type of his genus *Bisiphytes reticulatus* (a then newly proposed species) which came from Sombernon, Burgundy (east-central France), presumably from Jurassic strata. As indicated by the generic name, Montfort thought his specimen had two siphuncles but the

Fig. 9. Cross sections of the conch of species of *Cenoceras*. Redrawn from Pia (1914, pl. 9 [6]). *A*, *C. toarcensis* (d'Orbigny) after d'Orbigny, diameter 240 mm.; *B*, *C. jurensis* (Quenstedt) after Quenstedt, diameter 40 mm.; *C*, *C.* sp. ind. No. 6, after Rosenberg, diameter 50 mm.; *D*, *C. demonensis* (Gemmellaro) after M. Gemmellaro, diameter 40 mm.; *E*, *C. austriacus* (Hauer) after Hauer, diameter 230 mm.; *F*, *C. aratus* (Quenstedt) after Quenstedt, diameter 40 mm.; *G*, *C. meyrati* (Ooster) after Ooster, diameter 80 mm.; *H*, *C. terebratus* (Dumortier) after Dumortier, diameter 98 mm.; *I*, *C. pseudorugosus* (Pia) after Ooster, diameter 90 mm.; *J*, *C. mariani* (Gemmellaro) after M. Gemmellaro, diameter 46 mm.; *K*, *C. rugosus* (Buvignier) after Buvignier, diameter 75 mm.; *L*, *C. astacoides* (Young and Bird) after Dumortier, diameter 112 mm.; *M*, *C. intermedius* (Sowerby), diameter 200 mm.; *N*, *C. jourdani* (Dumortier) after Dumortier, diameter 130 mm.; *O*, *C. inornatus* (d'Orbigny) after d'Orbigny, diameter 85 mm.; *P*, *C.* sp. ind. No. 8, after Vadász, diameter 66 mm.; *Q*, *C. truncatus* (Sowerby) after Geyer, diameter 80 mm.

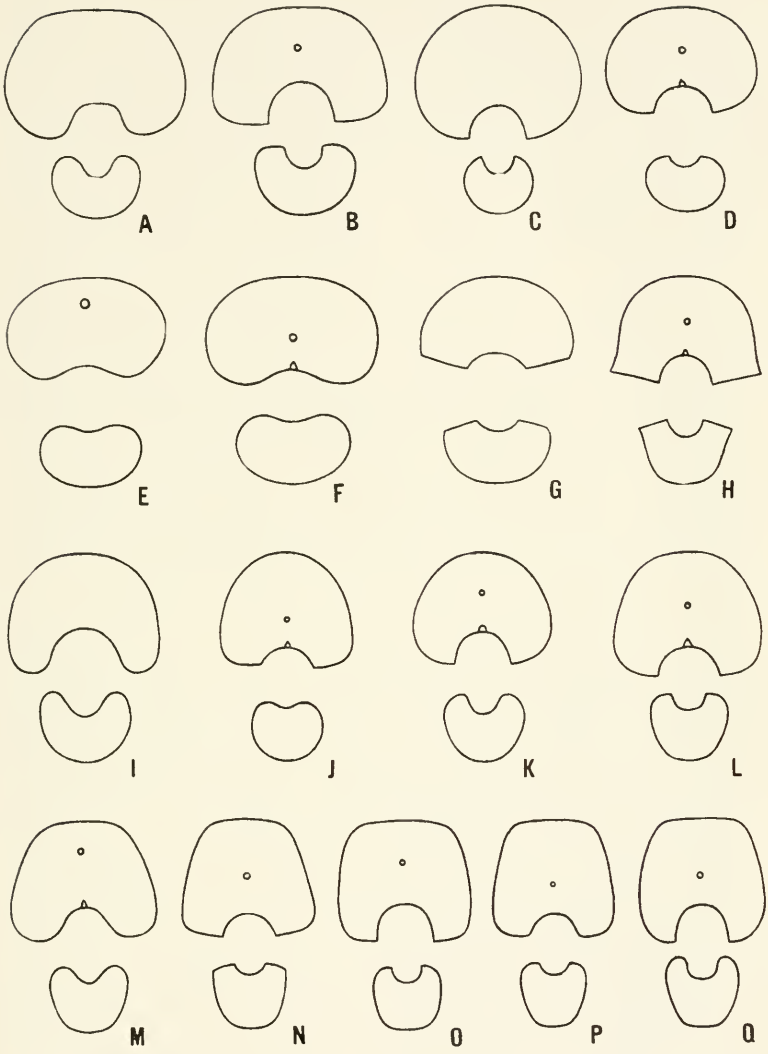

Figure 9

second "siphuncle" is undoubtedly an indentation of the dorsal lobe. The only illustration of *Bisiphytes reticulatus* is a rather crude sketch (reproduced here on Plate 25, fig. 3). It is not possible to recognize the specific features of the genotype of *Bisiphytes* from Montfort's description and/or his illustration; likewise the exact locality and horizon from which the specimen was collected is not known. For these reasons the genus *Bisiphytes* should not be used (a recommendation set forth by Teichert in 1940, p. 591, and in several written communications to the writer). A petition to suppress the generic name *Bisiphytes* is being made to the International Commission on Zoological Nomenclature. Abandonment of *Bisiphytes* leaves available the genus *Cenoceras* — type *Nautilus intermedius* d'Orbigny non Sowerby=*N. orbignyi* Prinz. I am in perfect agreement with Spath that the quadrate whorled *Cenoceras* cannot be separated from the rounder whorled *Bisiphytes*. My previous use of *Cenoceras* as a subgenus of *Bisiphytes* was an attempt to express the homogeneity of these two groups but I am now convinced that Teichert's recommendation to suppress *Bisiphytes*, because of the almost complete ambiguity surrounding the type species, will do much to clarify the taxonomy of these Jurassic nautiloids.

Fig. 10. Cross section of the conch of species of *Cenoceras* and *Pseudaganides*. Redrawn from Pia (1914, pl. 10, [7]). *A*, *C. quadrangularis* (Pia) after Pia, diameter 103 mm.; *B*, *C. balsamocrivellii* (Parona), after Parona, diameter 155 mm.; *C*, *C. distefanoi* (Gemmellaro) after M. Gemmellaro, diameter 52 mm.; *D*, *D. brancoi* (Gemmellaro) after M. Gemmellaro, diameter 60 mm.; *E*, *C. affinis* (Chapuis and Dewalque) after Chapuis and Dewalque, diameter 101 mm.; *F*, *C.* sp. ind. No. 5, after Rosenberg, diameter 32 mm.; *G*, *C. profundisiphites* (Prinz) after Prinz diameter 82 mm.; *H*, *C. tricarinatus* (Vadász) after Vadász, diameter 91 mm.; *I*, *C. anomphalus* (Pia) after d'Orbigny, diameter 90 mm.; *J*, *C.* sp. ind. No. 9, after Vadász, diameter 36 mm.; *K*, *C. chilensis* (Huppé) after Möricke, diameter 99 mm.; *L*, *C. amoretti* (Parona) after Parona, diameter 80 mm.; *M*, *C. breislacki* (Parona) after Parona, diameter 93 mm.; *N*, *C. egregius* (Pia) after Pia, diameter 207 mm.; *O*, *C. semistriatus* (d'Orbigny) after d'Orbigny, diameter 165 mm.; *P*. *Pseudaganides gravesiana* (d'Orbigny), diameter 240 mm.; *Q*, *C. schwalmi* (Prinz) after Prinz, diameter 89 mm.; *R*, *C. fischeranus* (Foord and Crick) after Foord, diameter 180 mm.; *S*, *C. pertextus* (Dumortier) after Dumortier, diameter 180 mm.; *T*, *C. spreaficoi* (Parona) after Parona, diameter 58 mm.; *U*, *C. pisanus* (Fucini) after Fucini, diameter 12 mm.

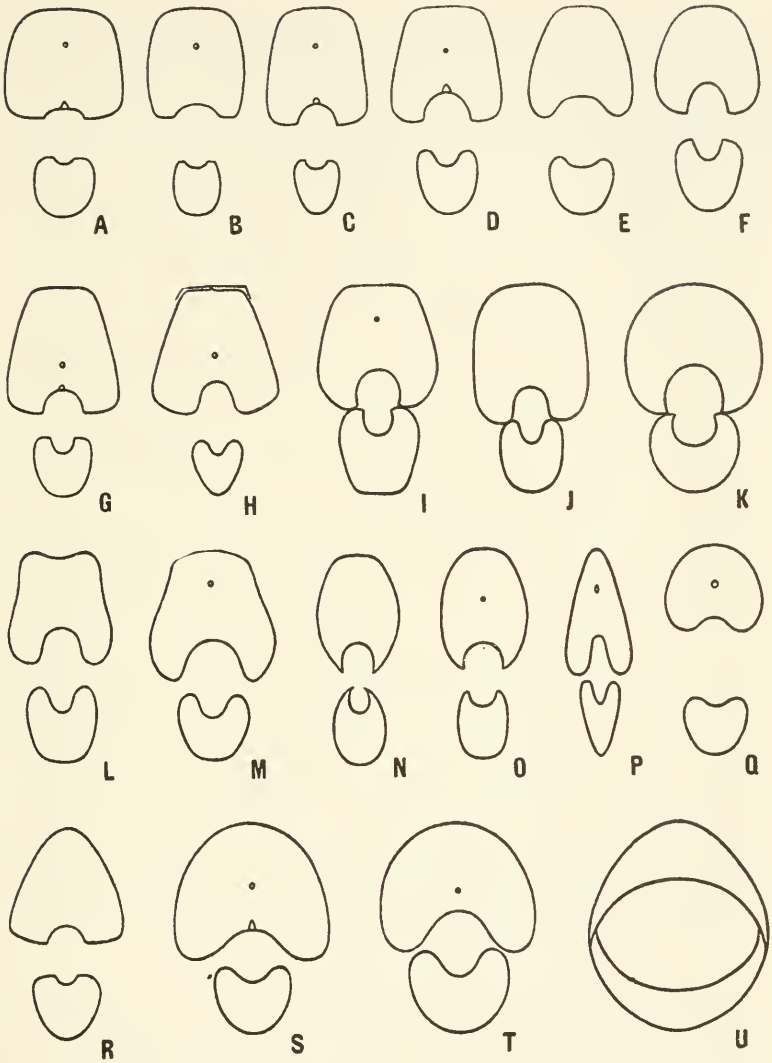

Figure 10

A precise morphological definition of *Cenoceras* is not possible because of the wide variability and range in conch shape and ornamentation. The suture is for the most part quite uniform having only slight ventral and lateral lobes. The variability in conch shape has been most admirably illustrated in a set of text figures by Pia (1914) which are reproduced here as Text Figures 8, 9, 10. Interpreting conch form as an expression of adaptation, these text figures clearly show the range of radiation in the group. The uniformity of the suture and types of ornamentational patterns supports the conclusion that all these species are part of a single genetic complex.

Spath (1927a) listed four other genera of Liassic nautiloids, namely: *Sphaeronautilus* Spath, *Digonioceras* Hyatt, *Ophionautilus* Spath, and *Hercoglossoceras* Spath. All these genera are now placed in synonymy of other forms. *Hercoglossoceras* is considered a synonym of *Pseudaganides*. The remaining genera (*Sphaeronautilus*, *Digonioceras*, and *Ophionautilus*) are considered to be synonyms of *Cenoceras*.

The type species of *Digonioceras* Hyatt, 1894, is *Digonioceras rotundum* Hyatt, non Crick, 1898, by original designation and not *Nautilus excavatus* J. de. C. Sowerby (1826, pl. 529, fig. 1; Pl. 9, figs. 3-5, of this report) as indicated by Spath (1927a, p. 21). The original description and illustration of *D. rotundum* (Hyatt, 1894, p. 549) leaves much to be desired. The type specimen, which is in the M.C.Z., is a juvenile of one volution and consists only of phragmocone. It measures 34 mm. in diameter; the width and height of the most adoral whorl are 23 mm. and 17.5 mm. respectively. The whorls are depressed and ovoid in cross section. The venter is broadly arched. The whorl sides are convex and grade onto the venter and the umbilical wall with no distinct shoulders to break the even curvature. The venter of the second camera is bluntly angular or fastigate. The rounded

aspect of the venter is apparent on the third camera. Adorally, the whorls become gradually more depressed producing the broad venter and narrowly rounded sides. The umbilicus is perforate, measuring approximately 2 mm. in diameter. The suture has very shallow ventral and lateral lobes, and no annular lobe. The siphuncle is in a subventral position. The shell is smooth except for fine growth lines that form a deep tongue-shaped sinus on the venter.

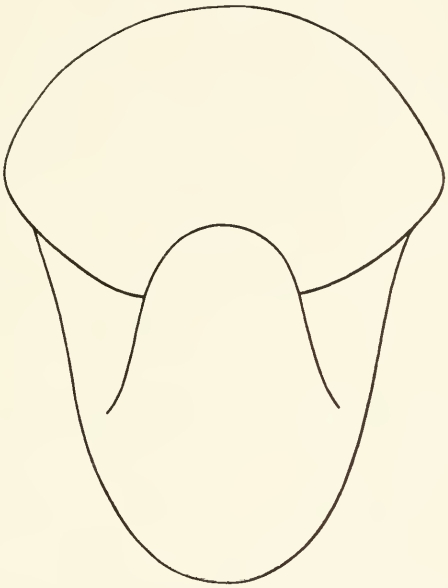

Fig. 11. *Cenoceras excavatus* (Sowerby). Diagrammatic cross-section of holotype represented by figures 1, 2, Plate 7. X 1.

Hyatt (1883, p. 288) included *Nautilus excavatus*, d'Orbigny in *Endolobus* and considered that species to be the latest survivor of that series. However, in 1894 (p. 549) he noted that there were significant differences between the Carboniferous *Endolobus* and the Jurassic species he placed in *Digonioceras*. My own study of Sowerby's type of *Nautilus excavatus* in the B.M.N.H. (figured here on Plate 7 and Text Figure 11) and Hyatt's type

of *Digonioceras rotundum* which is in the M.C.Z. lead me to conclude that it is not possible to tell whether or not these two species are congeneric in Hyatt's sense. *Digonioceras rotundum* is based on a juvenile specimen which is very generalized in its characters. The locality and geologic horizon of *D. rotundum* is not known, but Hyatt (1894, p. 549) writes, "It is obviously from the Oolite but the locality is not known."

The large funnel-shaped umbilicus of *Nautilus excavatus* is the principal character used by Hyatt and later by Spath to set this group aside as a separate generic category under the name *Digonioceras*. Other Middle Jurassic species which appear to be related to *Nautilus excavatus*, at least in the general character of the umbilicus, are *N. smithi* Foord and Crick, 1890, and *N. dispansus* Morris and Lycett, 1850. From the Lias, similar umbilical features are found in *Nautilus meyrati* Ooster (1858) (Fig. 9*G*) and in *N. terebratus* Dumortier (1874) (Fig. 9*H*). The umbilical shoulders of the latter species are flared and angular; the umbilical wall is broad and sloping toward the umbilicus. The group of *Nautilus excavatus* does not appear to have given rise to any later stock of nautiloids and is here interpreted as merely one (of the many) adaptive types produced in the early Jurassic within the *Cenoceras* complex. From an evolutionary viewpoint the group is merely a part or expression of the adaptive radiation or plastic phase found in the early Jurassic, and the group should be taxonomically treated as species of *Cenoceras*.

Ophionautilus Spath (1927), type species *Nautilus burtonensis* Foord and Crick, 1890 (illustrated here on Plate 6, and Text Figure 12), was differentiated on the basis of the very evolute, widely umbilicate conch. The type species is from the Inferior Oolite of England. In addition to the type species, *Nautilus zitteli* Gemmellaro (1886) of the lower Dogger of Sicily, *N. austriacus* Hauer (1856) (Fig. 9*E*) and *N. schwalmi* Prinz (1906) (Fig. 10*Q*) from the Liassic of the Alps and Hungary, respectively, belong to this species group. These species which have been or can be assigned to *Ophionautilus* are interpreted as evolute adaptations of the *Cenoceras* complex. These evolute elements did not give rise to any of the succeeding more stable evolutionary lines. *Nautilus burtonensis* Foord and Crick has an evolute, smooth, rather large conch. The whorl section is

wider than high. The venter is broadly rounded to slightly flattened; the whorl sides are rounded as are the umbilical shoulders. The umbilical wall is convex and steep. The umbilicus is broad and deep, exposing much of the inner whorls. The suture is only slightly sinuous with a shallow ventral and a shallow lateral lobe that includes the whole whorl side. The only markings on the shell are growth lines and they form a deep sinus on the venter. The siphuncle is more or less centrally

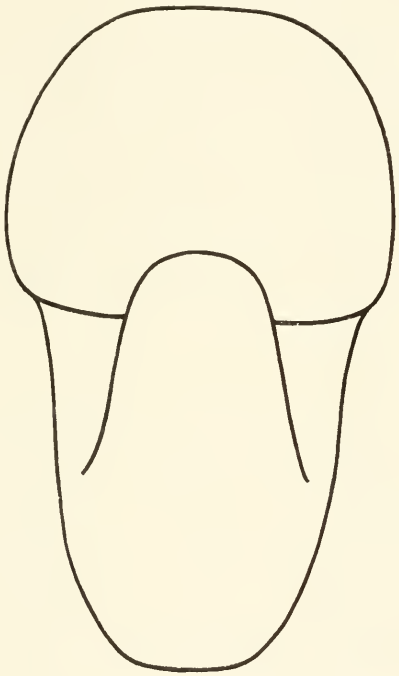

Fig. 12. *Cenoceras burtonensis* (Foord and Crick). Diagrammatic cross section of holotype represented by figures 1, 2, Plate 6, X 1.

located. The group of *Nautilus burtonensis* includes the most evolute adaptation of the *Cenoceras* complex but there is within this complex a nearly complete gradational series in degree of involution.

Whereas the group of *Nautilus burtonensis* includes the most evolute elements of the *Cenoceras* complex, the most involute form is *Nautilus pisanus* Fucini (1895, p. 328, pl. 13, fig. 5) from lower Liassic strata of Italy for which Spath (1927a, p. 21) established the genus *Sphaeronautilus* (Fig. 10*U*). In its arcestid-like shape *Nautilus pisanus* is indeed an extreme aberrant type. The conch is small and smooth. The suture has only a slight lobe on the ventral and lateral areas. There is not known at present a perfect gradational series from "typical" *Cenoceras* to the extremely involute *Nautilus pisanus*. However, its stratigraphic position and general morphological characters make it logical to consider *Nautilus pisanus* as the extreme involute development of the *Cenoceras* complex and the genus *Sphaeronautilus* is placed in synonymy of *Cenoceras*.

More species have been described for *Cenoceras* than for any other genus of post-Triassic nautiloids. Of the 96 species, two-thirds are Lias in age and the remaining third Middle Jurassic in age. *Cenoceras* is a truly cosmopolitan form being known from nearly all continental areas (Fig. 6). The species belonging to *Cenoceras* with their age and geographic distribution are listed below.

DISTRIBUTION OF SPECIES OF THE GENUS CENOCERAS

Species	Stratigraphic Distribution	Geographic Distribution
C. adneticus (Pia) 1914	Jurassic (Lias)	Austria
C. affinis (Chapuis and Dewalque) 1853	Jurassic (Lias)	Luxembourg
C. altisiphites (Prinz) 1906	Jurassic (Lias)	Hungary
C. amasianus (Gugenberger) 1928	Jurassic (Lias)	Turkey
C. amorettii (Parona) 1897	Jurassic (Lias)	Italy
C. anomphalus (Pia) 1914	Jurassic (Lias)	France
C. arariformis (Pia) 1914	Jurassic (Lias)	Austria
C. araris (Dumortier) 1869	Jurassic (Lias)	Europe

Species	Stratigraphic Distribution	Geographic Distribution
C. aratus (Quenstedt) 1846	Jurassic (Lias)	Germany
C. arthaberi (Gugenberger) 1928	Jurassic (Lias)	Turkey
C. astacoides (Young and Bird) 1828	Jurassic (Lias)	Europe
C. austriacus (Hauer) 1856	Jurassic (Lias)	Alps
C. baconicus (Vadász) 1911	Jurassic (Lias)	Hungary
C. balsamocrivellii (Parona) 1897	Jurassic (Lias)	Italy
C. bradfordensis (Crick) 1898	Jurassic (Bajocian)	England
C. brancoi (Gemmellaro) 1884	Jurassic (Lias)	Italy
C. breislacki (Parona) 1897	Jurassic (Lias)	Italy
C. burtonensis (Foord and Crick) 1890	Jurassic (Bajocian)	England
C. catonis (Gemmellaro) 1886	Jurassic (L. Dogger)	Sicily
C. chilensis (Huppé) 1854	Jurassic (Lias)	Chile
C. demonensis (M. Gemmellaro) 1911	Jurassic (Lias)	Sicily
?*C. dispansus* (Morris and Lycett) 1850	Jurassic (Bathonian)	England
C. distefanoi (Gemmellaro) 1884	Jurassic (Lias)	Italy
C. domeykus (d'Orbigny) 1842	Jurassic (Lias)	Chile
C. egregius (Pia) 1914	Jurassic (Lias)	Austria
C. ercycinus (Tagliarini) 1901	Jurassic (L. Dogger)	Sicily
C. excavatus (J. de C. Sowerby) 1826	Jurassic (Bajocian)	England
C. exiguus (Crick) 1898	Jurassic (Bajocian)	England

Species	Stratigraphic Distribution	Geographic Distribution
C. exterebratus (Crick) 1898	Jurassic (Bajocian)	England
C. fischeranus (Foord and Crick) 1890	Jurassic (Lias)	France
C. fourneti (Dumortier) 1874	Jurassic (Lias)	Europe
C. geyeri (Prinz) 1906	Jurassic (Lias)	Austria
C. hallstattensis (Spengler) 1919	Jurassic (Lias)	Austria
C. imlayi (Kummel) 1954	Jurassic (Bajocian)	Alaska
C. impendens (Crick) 1898	Jurassic (Bajocian)	England
C. inornatus (d'Orbigny) 1842	Jurassic (Lias)	Europe
E. intermedius (J. Sowerby) 1816	Jurassic (Lias)	Europe
C. jourdani (Dumortier) 1874	Jurassic (Lias)	Europe
C. julianus (Fucini) 1895	Jurassic (Lias)	Italy
C. jurensis (Quenstedt) 1858	Jurassic (Lias)	Europe
C. lineatus (J. Sowerby) 1813	Jurassic (Bajocian)	England
C. lineolatus (Foord and Crick) 1890	Jurassic (Lias and Bajocian)	England France
C. lupheri (Kummel) 1954	Jurassic (Bajocian)	Oregon (U.S.A.)
C. lutatii (Gemmellaro) 1886	Jurassic (L. Dogger)	Sicily
C. malherbii (Terquem) 1855	Jurassic (Lias)	Luxembourg
C. manissadjiani (Gugenberger) 1928	Jurassic (Lias)	Turkey
C. mariani (M. Gemmellaro) 1911	Jurassic (Lias)	Sicily
C. marii (Gemmellaro) 1886	Jurassic (L. Dogger)	Sicily

Species	Stratigraphic Distribution	Geographic Distribution
C. mazzarensis (Tagliarini) 1901	Jurassic (L. Dogger)	Sicily
C. meyrati (Ooster) 1858	Jurassic (Lias)	Alps
C. multiseptatus (Foord and Crick) 1890	Jurassic (Bajocian)	England
C. obesus (J. Sowerby) 1816	Jurassic (Bajocian)	England
C. obstructus (Deslongchamps) 1878	Jurassic (Bajocian)	France, England
C. orbignyi (Prinz) 1906	Jurassic (Lias)	Europe
C. ornatus (Foord and Crick) 1890	Jurassic (Bajocian)	England
C. ornatus var. *atanatensis* (Pia) 1914	Jurassic (Lias)	Austria
C. paretoi (M. Gemmellaro) 1911	Jurassic (Lias)	Sicily
C. perinflatus (Foord and Crick) 1890	Jurassic (Bajocian)	England
C. perornatus (Crick) 1894	Jurassic (Bajocian)	Western Australia
C. pertextus (Dumortier) 1867	Jurassic (Lias)	France Austria
C. pisanus (Fucini) 1895	Jurassic (Lias)	Italy
C. polygonalis (J. de C. Sowerby) 1826	Jurassic (Bajocian)	England
C. postriatus (Prinz) 1906	Jurassic (Lias)	Europe
C. profundisiphytes (Prinz) 1906	Jurassic (Lias)	Austria
C. pseudolineatus (Foord and Crick) 1890	Jurassic (Bajocian)	England
C. pseudorugosus (Pia) 1914	Jurassic (Lias)	Alpine Region
C. pseudotruncatus (Crick) 1921	Jurassic (Lias)	England
C. quadrangularis (Pia) 1914	Jurassic (Lias)	Austria
C. robustus (Foord and Crick) 1890	Jurassic (Lias)	France, Austria

Species	Stratigraphic Distribution	Geographic Distribution
C. rotundum (Hyatt) 1894	Jurassic (Bajocian?)	England
C. rotundum (Crick) 1898	Jurassic (Bajocian)	England
C. rugosus (Buvignier) 1852	Jurassic (Lias)	Europe
C. schlumbergeri (Terquem) 1855	Jurassic (Lias)	Luxembourg
C. schmidti (Giebel) 1852	Jurassic (Lias)	Germany
C. schwalmi (Prinz) 1906	Jurassic (Lias)	Hungary
C. secernendus (Pia) 1914	Jurassic (Lias)	Austria
C. semiornatus (Crick) 1898	Jurassic (Bajocian)	England
C. semistriatus (d'Orbigny) 1843	Jurassic (Lias)	France
C. semseyi (Prinz) 1904	Jurassic (Lias and L. Dogger)	Hungary
C. simillimus (Foord and Crick) 1890	Jurassic (Lias)	England, Austria
C. smithi (Foord and Crick) 1890	Jurassic (Bajocian)	England
C. spreaficoi (Parona) 1897	Jurassic (Lias)	Italy
C. steinmanni (Möricke) 1894	Jurassic (Middle)	Chile
C. stoppanii (Parona) 1897	Jurassic (Lias)	Italy
C. striatus (J. Sowerby) 1817	Jurassic (Lias)	Europe
C. sturi (Hauer) 1856	Jurassic (Lias)	Alpine Region
C. subrotundus (Crick) 1898	Jurassic (Bajocian)	England
C. subtruncatus (Prinz) 1906	Jurassic (Lias)	France
C. terebratus (Dumortier) 1874	Jurassic (Lias)	France, England

Species	Stratigraphic Distribution	Geographic Distribution
C. thyrrenus (Tagliarini) 1901	Jurassic (L. Dogger)	Sicily
C. toarcensis (d'Orbigny) 1849	Jurassic (Lias)	France, Germany,
C. tricarinatus (Vadász) 1911	Jurassic (Lias)	Austria
C. truncatus (Sowerby) 1816	Jurassic (Lias)	Europe
C. waageni (Gemmellaro) 1886	Jurassic (L. Dogger)	Sicily
C. zignoi (Gemmellaro) 1886	Jurassic (L. Dogger)	Sicily
C. zitteli (Gemmellaro) 1886	Jurassic (Middle)	Sicily

Genus EUTREPHOCERAS Hyatt, 1894

Eutrephoceras Hyatt, 1894, p. 555.
Eutrephoceras Reeside, 1924, p. 2.
Eutrephoceras Reeside, 1927b, pp. 6, 7.
Eutrephoceras Miller and Thompson, 1933, pp. 300-304.
Eutrephoceras Spath, 1927a, pp. 21, 24.
Eutrephoceras Spath, 1927b, pp. 425, 426, 428.
Eutrephoceras Stenzel, 1940, pp. 738-742.
Eutrephoceras Miller, 1947, pp. 26-39.
Eutrephoceras Miller, 1951, pp. 33-36.

The genus *Eutrephoceras* represents the long-lived and persistent stock arising from the lower Jurassic *Cenoceras* complex and is considered to be the root from which most of the remaining Cretaceous and Tertiary nautiloids, excepting the Cymatoceratinae, are derived. It is most similar to *Cimomia* and *Nautilus*. *Cimomia* arose from *Eutrephoceras* in the Upper Jurassic or Cretaceous and is in itself the root stock of the Hercoglossinae. *Cimomia* differs from *Eutrephoceras* in the greater sinuosity of the suture, but many intermediate forms are known.

Thus the interpretation of *Eutrephoceras* presented here visualizes a persisting, slowly evolving stock consisting of generally involute, smooth forms with straight or nearly straight sutures, and a conch that is generally subglobular but can be quite compressed or depressed. The rather wide variation in the shape of the conch is illustrated in Text Figure 13.

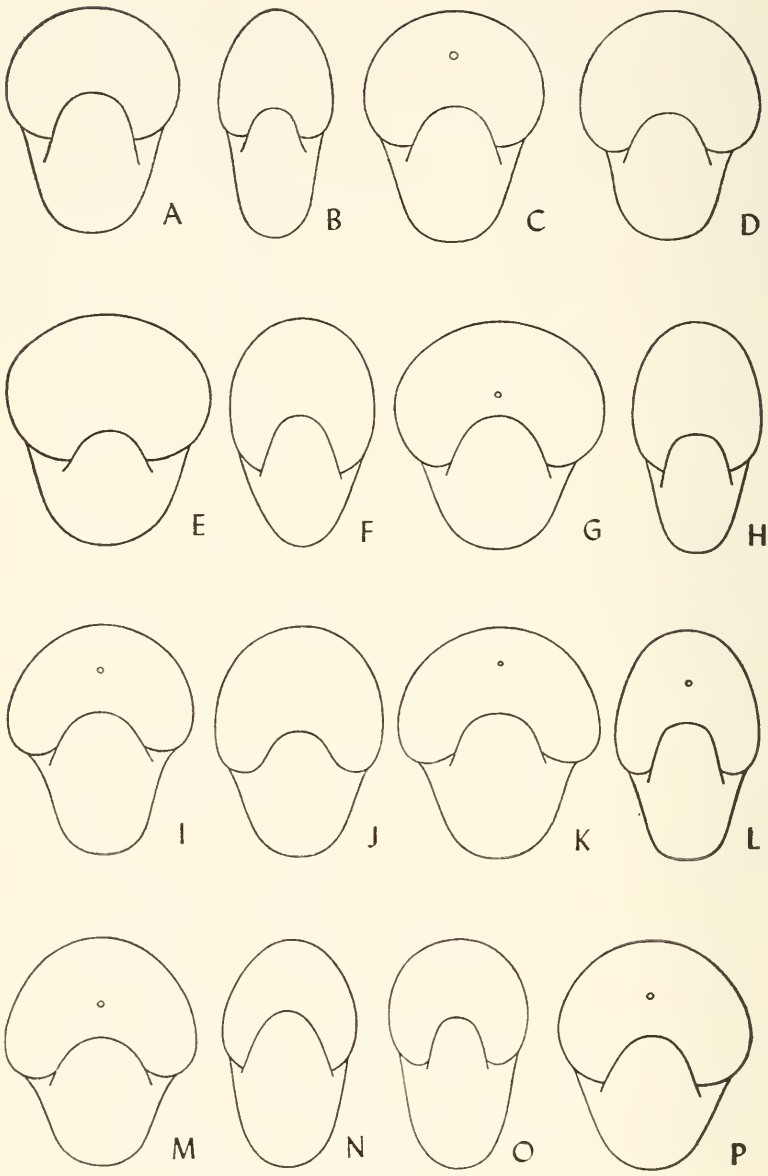

Figure 13

Probably the commonest and most widespread genus of post-Triassic nautiloids is *Eutrephoceras*. To date, approximately 89 species are recognized ranging in age from the Jurassic to the Miocene; of these, 6 species are Jurassic in age, 39 Cretaceous and 44 from the Tertiary.

Miller has recently described the American Tertiary species of *Eutrephoceras* and his comprehensive diagnosis of the genus is quoted here (1947, p. 27): "Conch nautiliconic and typically subglobular; whorls reniform in cross section, broadly rounded ventrally and laterally, and moderately deeply impressed dorsally. Aperture marked ventrally by a broad shallow rounded hyponomic sinus. Umbilicus small and inconspicuous; umbilical shoulders low and rounded. Surface of conch smooth or essentially so. Septa moderately convex apicad; sutures of typical forms slightly sinuous, but at least the external sutures of some forms are essentially straight. An annular lobe is present in some forms but not in the genotype. Siphuncle small, circular in cross section, and orthochoanitic in structure; its position varies considerably in the different species, but in no case is it marginal."

The large number of species of *Eutrephoceras* reflects their general abundance and widespread distribution geographically and stratigraphically. The wide variability in conch shape, degree of involution, and inflection of the suture suggest a wide adaptive range for this genetic stock. Probably in no other

Fig. 13. Cross sections of the conch of *A*, *Eutrephoceras cyclotus* (Oppel) from Zittel 1868, pl. 3, fig. 2a, diameter 117 mm.; *B*, *E. boissieri* (Pictet) 1867, pl. 8, fig. 4b, diameter 63 mm.; *C*, *E. subinflatus* (d'Orbigny) 1850, from d'Orbigny 1840, pl. 37, fig. 2, diameter 88 mm.; *D*, *E. jonesi* Miller and Thompson, from Stenzel 1940, fig. 115, diameter 225 mm.; *E*, *E. piersantii* (Sergio) 1933, pl. 2, fig. 4b, diameter 144 mm.; *F*, *E. justus* (Blanford), from Stoliczka 1866, pl. 93, fig. 2a, diameter 64 mm.; *G*, *E. dekayi* (Morton), from Stenzel 1940, fig. 115, diameter 46 mm.; *H*, *E. victorianum* Teichert 1947, fig. 5, diameter 102 mm.; *I*, *E. reesidei* Stenzel 1940, fig. 115, diameter 14.6 mm.; *J*, *E. neubergicus* (Redtenbacher) from Schlüter 1876, pl. 48, fig. 4, diameter 90 mm.; *K*, *E. dekayi* (Morton) from Stenzel 1940, fig. 115, diameter 85 mm.; *L*, *E. sloani* Reeside from Stenzel 1940, fig. 115, diameter 120 mm.; *M*, *E. carolinense* Kellum, from Stenzel 1940, fig. 115, diameter 20.7 mm.; *N*, *E. lentiformis* (Stoliczka) 1866, pl. 93, fig. 1a, diameter 74 mm.; *O*, *E. cookanum* (Whitfield), Stenzel 1940, fig. 115, diameter 220 mm.; *P*, *E. laverdei* Durham 1946, pl. 63, fig. 4, diameter 61 mm.

generic group are the recognized species so gradational in character and generally lacking in objectivity. Variability studies of large populations would be extremely helpful in assessing the many species groups.

Since *Eutrephoceras* is interpreted as the basic persisting stock derived from the *Cenoceras* complex, its relationships to the other genetic groups are discussed in detail under each of these derived groups and need not be repeated here.

A similar long-persisting, smooth, involute, generalized stock is represented in the Permo-Carboniferous and Triassic by the *Liroceras-Paranautilus* trend. From this particular trend was derived the Upper Triassic Clydonautilidae which is a stock adapted for sinuosity of the suture; a homeomorphous development of the Hercoglossinae.

Eutrephoceras is world-wide in distribution and ranges in age from the Upper Jurassic into the Miocene.

DISTRIBUTION OF SPECIES OF THE GENUS EUTREPHOCERAS

Species	Stratigraphic Distribution	Geographic Distribution
E. ahltenensis (Schlüter) 1876	Cretaceous (Upper)	Germany
E. alcesense Reeside, 1927	Cretaceous (Upper)	Montana (U.S.A.)
E. allani (Fleming) 1945	Oligocene ?	New Zealand
E. allioni (Michelotti) 1840	Miocene	Italy, Malta
E. altifrons (Chapman) 1915	Miocene	Australia
E. archiacianus d'Orbigny 1840	Cretaceous	France
E. balcombensis (Chapman) 1915	Miocene	Australia
E. bellerophon (Lundgren) 1867	Cretaceous (Danian)	Sweden
E. berryi Miller, 1947	Eocene	North Carolina (U.S.A.)
E. blanfordi (Douvillé) 1929	Eocene	Pakistan
E. boissieri (Pictet) 1867	Cretaceous (Lower)	Switzerland, Algeria
E. bouchardianus (d'Orbigny) 1840	Cretaceous (Albian)	France
E. bryani (Gabb) 1877	Eocene	New Jersey (U.S.A.)

Species	Stratigraphic Distribution	Geographic Distribution
E. burkarti (Castillo and Aguilera) 1895	Jurassic (Tithonian)	Mexico
E. butonensis (Martin) 1933	Oligocene	East Indies
E. carolinense Kellum, 1926	Eocene	North Carolina (U.S.A.)
E. centralis (J. Sowerby) 1812	Eocene	England, Germany
E. charpentieri (Leymerie) 1851	Cretaceous (Upper)	France
E. clementinus (d'Orbigny) 1840	Cretaceous (Albian)	England France
E. cookanum (Whitfield) 1892	Eocene	New Jersey (U.S.A.)
E. crassus (Schafhäutl) 1863	Eocene	Bavaria
E. cyclotus (Oppel) 1865	Jurassic (Tithonian)	Moravia
E. dartevellei Miller 1951	Eocene	Landana, West Africa
E. darupensis (Schlüter) 1876	Cretaceous (Senonian)	Germany
E. decipiens (Michelotti) 1861	Miocene	Italy
E. dekayi (Morton) 1834	Cretaceous (Upper)	U.S.A.
E. depressus (Binckhorst) 1861	Cretaceous (Maestrichtian)	Belgium
E. dersertorum (Quaas) 1902	Cretaceous (Danian)	Libya
E. dietrichi (Zwierzycki) 1914	Cretaceous (Neocomian)	East Africa
E. douvillei Spath, 1927	Jurassic (Oxfordian)	Egypt
E. dubalcni (Peyrot) 1932	Miocene	France
E. euthymi (Pictet) 1867	Cretaceous (Lower)	France, Switzerland
E. expansum (J. de C. Sowerby) 1824	Cretaceous (Cenomanian)	England
E. faxoense Hyatt, 1894	Cretaceous (Danian)	Denmark
E. felix (Chapman) 1915	Miocene	Australia

Species	Stratigraphic Distribution	Geographic Distribution
E. flammeus (Ronchetti) 1947	Cretaceous (Maestrichtian)	Tripolitania
E. francomontanus (Kuhn) 1939	Jurassic (Upper)	Germany
E. geelongensis (Foord) 1891	Miocene	Australia
E. gosavicus (Redtenbacher) 1873	Cretaceous (Upper)	Austria
E. hannai Vokes, 1937	Eocene	California (U.S.A.)
E.? hallidayi (Waring) 1914	Paleocene	California (U.S.A.)
E. hendersoni (Etheridge) 1901	Cretaceous (Lower)	Queensland, Australia
E. indicum (Spengler) 1910	Cretaceous (Upper)	India
E. izumoensis Yokoyama, 1913	Tertiary	Japan
E. japonicus (Shimizu) 1926	Eocene	Japan
E. javanus (Martin) 1879	Tertiary	Java
E. johnsoni Miller, 1947	Paleocene ?	Alabama (U.S.A.)
E. jonesi Miller and Thompson, 1933	Paleocene	Alabama (U.S.A.)
E. labechi (d'Archiac and Haime) 1854	Eocene	Pakistan
E. lavcrdei Durham, 1946	Cretaceous (Aptian)	Colombia
E. leonei (Negri) 1934	Eocene	Libya
E. marksi Miller, 1947	Eocene	California (U.S.A.)
E. marucoensis (Giovine) 1950	Cretaceous (Hauterivian)	Argentina
E. metafleuriausi (Douvillé) 1929	Cretaceous (Upper)	N. Africa
	L. Tertiary	Pakistan
E. montanensi Kummel, 1954	Jurassic (Callovian)	Montana (U.S.A.)
E. montmollini (Pictet and Campiche) 1859	Cretaceous (Albian)	Switzerland France
E. neubergicus (Redtenbacher) 1873	Cretaceous (Upper)	Austria
E. oregonense Miller, 1947	Eocene	Oregon (U.S.A.)

Species	Stratigraphic Distribution	Geographic Distribution
E. ovoideum Criek, 1907	Cretaceous	Zululand
E. parisiensis (Deshayes) 1866	Eocene	France
E. perlatus (Morton) 1834	Cretaceous (Upper)	Alabama (U.S.A.)
E. piersantii (Sergio) 1933	Oligocene	Italy
E. planoventer Stephenson, 1941	Cretaceous (Upper)	Tennessee, Texas (U.S.A.)
E. quadrilineatus (Favre) 1869	Cretaceous (Upper)	Germany
E. reesidei Stengel, 1940	Eocene	Texas (U.S.A.)
E. regalis (J. de C. Sowerby) 1843	Eocene	England
E. regularis (Schafhäutl) 1863	Eocene	Bavaria
E. restrictus (Griepenekerl) 1889	Cretaceous (Senonian)	Germany
E. resupinatus (Redtenbacher) 1873	Cretaceous (Upper)	Austria
E. sanfilippoi (Sorrentino) 1932	Cretaceous (Maestrichtian)	Tripolitania
E. simile Spath, 1953	Cretaceous (Upper)	Graham Land
E. sloani Reeside, 1924	Eocene	South Carolina (U.S.A.)
E. sphaericum (Forbes) 1846	Cretaceous	India
E. staadti (Cossmann) 1902	Eocene	France
E. stephensoni (Dickerson) 1914	Paleocene	California (U.S.A.)
E. stricteumbilicatus (Stehépinsky) 1943	Oligocene	Turkey
E. subinflatus (d'Orbigny) 1850	Jurassic (Kimmeridgian)	France
E. sublaevigatum (d'Orbigny) 1840	Cretaceous (Upper)	England, India, Madagascar, Libya
E. subplicatum (Philippi) 1895	Cretaceous (Upper)	Argentina, Chile
E. szontaghi (Vogl) 1910	Eocene	Hungary
E. thomi Reeside, 1927	Cretaceous (Upper)	Montana (U.S.A.)
E. tumescens (Frauscher) 1895	Eocene	Austria

Species	Stratigraphic Distribution	Geographic Distribution
E. uitenhagense Spath, 1930	Cretaceous (Valanginian)	South Africa
E. umbilicaris (Deshayes) 1835	Eocene	France
E. urbanus (Sowerby) 1843	Eocene	England
E. vastus (Kner) 1850	Cretaceous (Upper)	Poland
E. vicentinus (Oppenheim) 1901	Tertiary (Lower)	Italy
E. victorianum (Teichert) 1943	Eocene	Australia
E. vinassai (Venzo) 1937	Oligocene	Italy

Genus PSEUDOCENOCERAS Spath, 1927

Type species. Nautilus largilliertianus d'Orbigny, 1840, pl. 18 (by original designation). Plesiotype illustrated on Plate 10, figs. 3, 4.

This genus can be diagnosed as follows: Conch involute, compressed, smooth. Whorl section subrectangular, venter broad, flattened, ventral shoulders rounded. Whorl sides flattened, subparallel. Umbilical shoulders rounded, umbilical wall nearly vertical. The suture is only slightly sinuous, essentially straight across the venter and with a broad, generally shallow, lateral lobe. The siphuncle is subcentral in position, that is, closer to the dorsum.

As stated by Spath (1927a, p. 24), "*Pseudocenoceras* is easily distinguished from its Cretaceous contemporaries by its steep umbilical edge, truncated whorl-shape, entomarginal siphuncle and reclined septal edges."

The Cretaceous contemporaries of *Pseudocenoceras* include members of the Cymatoceratinae, the Hercoglossinae, *Eutrephoceras*, and *Carinonautilus*. The smooth conch and simple suture would ally *Eutrephoceras* and *Pseudocenoceras;* all of the other generic groups are specialized forms trending on quite different patterns.

There are only 8 species of Cretaceous nautiloids that can be assigned to *Pseudocenoceras*, and all are for the most part very similar. The type species is a common form in Cretaceous strata of England and France. *Nautilus berriasensis* Pictet (1867) from Lower Cretaceous strata of France appears to be closely allied to *Nautilus largilliertianus* but has a more central siphuncle. *Nautilus lehardyi* Binckhorst (1861) is a quite aberrant

form with subangular ventral shoulders and a concave venter. It is placed in *Pseudocenoceras* with question.

Pseudocenoceras is a fairly common form in Cretaceous rocks of Europe from England to the Crimea. One species, *Nautilus applanatus* Wanner (1902), is from the Upper Cretaceous of Libya. A list of the species of *Pseudocenoceras*, their age, and geographic distribution is given below.

DISTRIBUTION OF SPECIES OF THE GENUS PSEUDOCENOCERAS

Species	Stratigraphic Distribution	Geographic Distribution
P. applanatus (Wanner) 1902	Cretaceous (Upper)	Libya
P. berriasensis (Pictet) 1867	Cretaceous (Lower)	France
P. campichei (Karakasch) 1907	Cretaceous (Lower)	Crimea
P. fittoni (Sharpe) 1853	Cretaceous (Upper)	Europe
P. galicianus (Alth) 1850	Cretaceous	Poland
P. largilliertianus (d'Orbigny) 1840	Cretaceous (Cenomanian)	Europe
P.? lehardyi (Binckhorst) 1861	Cretaceous (Maestrichtian)	Belgium
P. pictet (Karakasch) 1907	Cretaceous (Lower)	Crimea

Genus CARINONAUTILUS Spengler, 1910

Type species. Carinonautilus ariyalurensis Spengler, 1910, p. 149, pl. 14, figs. 1 a–e (monotypic). Illustrated here on Plate 11.

The only data available on this monotypic genus are the description and illustration of the type species. However, from this source the following diagnosis is made. The conch is very involute, compressed, and much higher than wide. The umbilicus is small and shallow. The whorl sides are broadly rounded and converge toward the venter. A distinct furrow aligns the ventral shoulder. The venter has a prominent rounded keel that on the adoral part of the living chamber is much broader and is divided by a median furrow. The umbilical shoulders are broadly rounded. The widest part of the whorl section is just ventral of the umbilical shoulders. The suture is only slightly convex.

The only markings on the shell are growth lines which form a deep sinus over the venter. The position of the siphuncle is not known.

At a diameter of 1.5 cm. the venter is not yet keeled but merely sharply rounded. At 3 cm. the single prominent keel is present, and at 6 cm. diameter the median furrow is well developed on the widened keel.

The measurements of the type species are as follows (Spengler, 1910, p. 149):

Diameter	93 mm.
Height of last whorl	54 mm.
Width of umbilicus	5.5 mm.
Width of last whorl	32 mm.

Spengler (1910, p. 149) recognized the uniqueness of this species and suggested that it was derived from *Nautilus angustus* Blanford (=*Cimomia*) by sharpening of the ventral area. Contemporaneous forms include members of the Cymatoceratinae, Hercoglossinae, *Eutrephoceras* and *Pseudocenoceras*. I am in essential agreement with Spengler on the phylogenetic position of *Cariñonautilus* but would derive them from *Eutrephoceras*, which is here considered the persistent evolving stock. There is slight difference between the eutrephoceratid stock and the cimomids. The eutrephoceratids show great variability in their smooth, involute conchs and appear to be the only evolutionary reservoir available to give rise to *Carinonautilus*.

This monotypic genus is known only from the Ariyalur group (Campanian) of the Trichinopoly district of southeast India.

Genus OBINAUTILUS Kobayashi, 1954

Type species. Obinautilus pulchra Kobayashi, 1954b. Type illustration reproduced on Plate 9, figs. 1, 2.

Kobayashi's description of his new monotypic species and genus is quoted below. The specimen is 78 mm. in diameter; last whorl 25 mm. in width, 46 mm. in height and 35 mm. in median height.

"Shell discoidal, compressed laterally, rapidly coiling and quite involute; umbilicus almost closed, if not completely; flanks a little convex, but nearly parallel in the inner half and inclined abruptly near the umbilicus; ventral sinus shallow but fairly

broad and provided with an obtuse peripheral carina on each side which is subangulated inside but outwardly merges with the flank.

"Radial ribs narrow, flattopped, separated by narrow and shallow grooves and frequently branching distally by insertion of fine grooves. These ribs and grooves distinctly bent forward from the umbilicus, nearly straight or even slightly concave backward in the broad flank, swing back a little near the venter and moderately sinuated behind on the venter. The curvature of these ribs is very similar to the growth lines of living *Nautilus*."

Kobayashi based the above description on a single well-preserved specimen. The shell is very well preserved and he (Kobayashi) notes "its deep and light brown shades must be the original colour pattern." Unfortunately, neither the suture nor position of the siphuncle was observed. The ribbing described by Kobayashi appears to be accentuated growth lines rather than the type of ribbing that is characteristic of the Cymatoceratinae.

The most characteristic feature of *Obinautilus* is the shallow but distinct ventral furrow. Because of this modification of the periphery, Kobayashi rightly pointed to possible affinities with the Paracenoceratidae. However, I agree completely with Kobayashi that *Obinautilus* should be considered a development of the Nautilinae rather than derived from any member of the Paracenoceratinae. Since the suture and position of the siphuncle are not known, this interpretation will have to remain tentative until more data become available.

Obinautilus pulchra is known from one specimen collected at a cutting between Aburatsu and Obi towns in the Province of Hyuga (Miyazaki Pref.), Japan, on the occasion of the highway operation. The locality is situated in the pre-Miocene terrain where the Nichinan formation containing the Oligocene Ashiya fauna lies unconformably beneath the Miocene Aburatsu formation (Kobayashi, 1954b, p. 183).

Genus NAUTILUS Linné, 1758

Type species. Nautilus pompilius Linné.

The interpretation of the scope of the genus *Nautilus* has changed considerably since its formal introduction by Linné.

In the early period of paleontological research on this group of tetrabranchiate cephalopods nearly all species were placed in the single genus *Nautilus*. Gradually as more and more genera were proposed, *Nautilus* became a waste-basket genus for unassigned forms. The greater amount of attention paid to Paleozoic nautiloids soon pre-empted the use of the genus *Nautilus* for species of that age. The genus has persisted for most species of Mesozoic and Tertiary nautiloids until rather recently. At the present, for instance, Miller (1951, p. 32) restricts *Nautilus* to only the Recent species and all of the Tertiary forms previously assigned to *Nautilus* are placed in *Eutrephoceras* or *Cimomia*. In this interpretation I am in full agreement. *Eutrephoceras* is the persisting stock out of the *Cenoceras* complex in Upper Jurassic time that shows no particular evolutionary trends from its time of origin to the time of its apparent extinction in the late Tertiary. It is the longest-lived single genetic stock of post-Triassic nautiloids, and was ancestral to several other aberrant groups, namely *Pseudocenoceras*, *Carinonautilus*, and *Obinautilus*. It is also ancestral to *Cimomia* of the Hercoglossinae which developed into an extremely abundant and diverse evolutionary complex. There appear to be no records of any Pliocene or Pleistocene nautiloids. Aside from *Aturia*, all other species of nautiloids seem to be more closely related to the eutrephoceratid evolving stock than to modern *Nautilus*. The number of species and specimens of Miocene nautiloids is still very few. However, with the above interpretation *Nautilus* is thought to arise from the eutrephoceratid stock at some time in the mid or late Tertiary.

The biology and ecology of modern *Nautilus* has been very ably summarized by Stenzel (1948, 1952). Similar comprehensive discussions of the morphology, etc., can be found in Miller (1947). The extensive literature on modern *Nautilus* is covered in the bibliographies of Stenzel's and Miller's papers.

Three species of living *Nautilus* are generally recognized, namely *N. pompilius* (with the umbilicus practically obliterated by the deposition of callus) *N. macromphalus* (with an open imperforate umbilicus), and *N. umbilicatus* (with an open finely perforate umbilicus) (Miller 1947, p. 13). Several "varieties" of *N. pompilius* are recognized but their significance and relationships are poorly known. To the above three species, Iredale

(1944) has added two new species, namely *N. alumnus,* from off Queensland and New South Wales, and *N. repertus* from off Western Australia.

Living *Nautilus* is restricted to the southwest Pacific from South Australia to the southern Philippines and eastward to the Fiji Islands. Stenzel (1948, p. 84) gives a good summary of the known records for live specimens of *Nautilus.*

Subfamily PSEUDAGANIDINAE nov.

This new subfamily is established for two genera of mainly Jurassic age that include adaptive types characterized by great sinuosity of the suture. These genera are *Pseudaganides* Spath, and *Pseudonautilus* Meek which Spath (1927) had previously included in his family Hercoglossidae. As is discussed in more detail below, *Pseudaganides* is considered to be a direct radiation from the *Cenoceras* complex in the Lower Jurassic; by the Upper Jurassic it was a widely distributed form in the European geosynclinal areas and showed a wide variation in conch form and suture. The group did not survive into the Cretaceous. Sometime during the Upper Jurassic an offshoot from *Pseudaganides* developed, characterized mainly by greater elaboration of the suture, that is, the formation of a deeper ventral lobe and angular lateral lobes. Species of this genus range into the Lower Cretaceous.

In the Carboniferous to Recent history of the nautiloids there were four distinct adaptive trends built around elaboration of the suture. As would be expected, there are many homeomorphous forms between these adaptive trends. Each of these trends had its origin in long-persisting, smooth, generalized stocks with very simple, nearly straight sutures. The duration of each of these trends is likewise somewhat limited. The Permian trend is known only through a single species of the genus *Permoceras* from Middle Permian strata of Timor. The Triassic radiation is mainly Upper Triassic (Carnian-Norian) in age. The Jurassic trend, represented by Pseudaganidinae, is Lower Jurassic to Lower Cretaceous in age with the principal radiation in the Upper Jurassic. The last such trend, that of the Hercoglossinae and Aturinae, is Upper Cretaceous to mid-Tertiary in range with the principal radiation in the Lower Tertiary.

Genus PSEUDAGANIDES Spath, 1927

Pseudaganides Spath, 1927a, pp. 22, 25.
Hercoglossoceras Spath, 1927a, pp. 22, 26.
Nautilus (*Pseudaganides*) Jeannet, 1951, pp. 17-21.
Type species. Nautilus kutchensis Waagen, 1873, pl. 3, fig. 4 (Plate 28, figures 3, 4 of this report). Type by original designation.

When Spath (1927a, p. 22) established this genus the only remark he made as to its characters was the following statement: "*Pseudaganides,* which comprises the early 'aganitici', like *Somalinautilus,* has its origin in '*Cenoceras*' and includes, for example, the large *subsinuatus* group of the Inferior Oolite, as already mentioned." In his discussion of the type species, *Pseudaganides kutchensis* (Waagen), Spath (1927a, pp. 34-35) mentions the following species as belonging to this genus: *N. aganiticus* Schlotheim, *N. schlotheimi* Loesch (=*Nautilus* (*Hercoglossa*) *aganiticus* Foord and Crick, 1890b, p. 394, fig. 1), and *N. ammoni* Loesch; he also included with question *N. girardoti* de Loriol and *N. subbiangulatus* d'Orbigny (=*Nautilus biangulatus* d'Orbigny, 1845, pl. 34, figs. 1-3).

There are approximately 40 species of Jurassic nautiloids with "goniatitic" sutures. Besides the "aganitici" included by Spath in *Pseudaganides,* he established the genus *Hercoglossoceras* [type species — *Hercoglossa* ('*gravesiana* (d'Orbigny) var.') *kochi* (Prinz)], a highly compressed form. *Pseudonautilus* was established by Meek for *Nautilus geinitzi* Oppel (*in* Zittel, 1868), and is characterized by a pointed lateral lobe and a very deep ventral lobe. A number of species from the Upper Jurassic (recently discussed by Loesch, 1914), Spath tentatively assigns to *Hercoglossa* (principally an Upper Cretaceous-Eocene development) though he does mention that they probably represent an independent development.

My own studies lead me to conclude that all of the Jurassic nautiloids with "goniatitic" sutures are part of a single evolutionary line developed from some compressed elements of "*Cenoceras*" and this line is quite independent of the later hercoglossid development.

The type species of *Pseudaganides* — *N. kutchensis* — comes from the Middle Chari group (*anceps* zone) of Kachh (Cutch) Pakistan. The type measures 47 mm. in diameter, 28 mm. for

length of whorl, 27 mm. as width of the whorl, and the umbilicus is 5 mm. across. Waagen's illustration is reproduced here on Plate 28, figures 3, 4. The form of the shell is involute with a somewhat rectangular whorl section with flattened sides and venter. The greatest width of the whorl is near the umbilicus. The suture has a prominent lateral lobe and a saddle next to the umbilicus. The suture is projected toward the venter and has a shallow lobe on the venter. The shell has fine longitudinal strigation and growth lines. The strigations disappear towards the aperture.

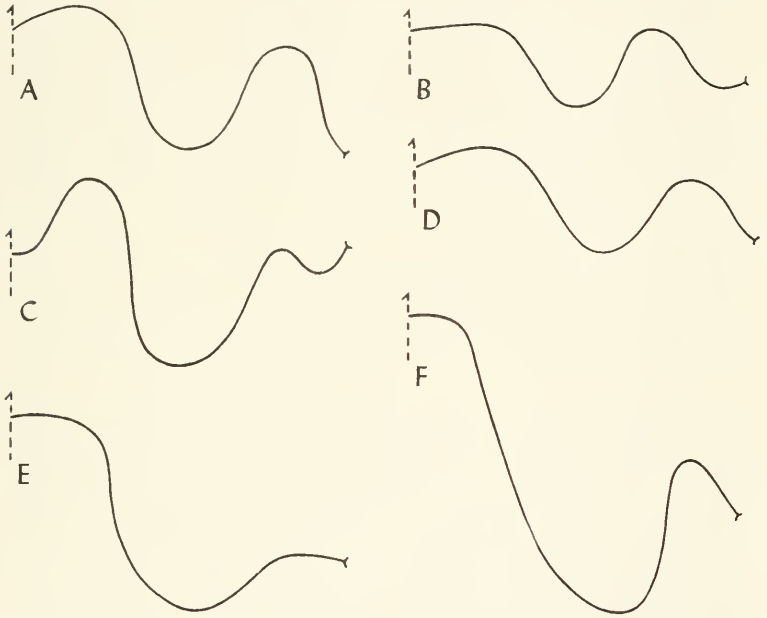

Fig. 14. Diagrammatic representation of sutures of *A*, *Pseudaganides brunhuberi* (Loesch) 1914, fig. 5c; *B*, *P. franconicus* (Oppel) from Loesch 1914, fig. 1a; *C*, *P. subbiangulatus* (d'Orbigny) 1843, from d'Orbigny 1850, pl. 34, fig. 3; *D*, *P. rogeri* (Loesch) 1914, fig. 3a; *E*, *P. pellerensis* (Vialli) 1937, fig. 1a; *F*, *P. sinuatus* (Sowerby), from Vialli, 1937, fig. 1a. All figures greatly reduced.

From the Carboniferous to the Tertiary, evolutionary trends, formulated on a complication of the suture, have occurred re-

peatedly. In most cases it can be established that such evolutionary lines arose from ancestors with essentially uncomplicated (nearly straight) sutures. Many of these evolutionary lines are represented by a single or very few species. However, some groups as the Triassic Clydonautilidae have large numbers of species. In genera such as *Clydonautilus* and *Proclydonautilus* there is a constancy in the pattern of the suture with, of course, a degree of modification in shape and depth of the lobes, etc.: there is, however, a very striking difference or range of variation in the shape of the conch (see Kummel, 1953c, figs. 38, 40, 41). This suggests that the genetic complex governing the nature of the suture is less adaptive than the shape of the conch. Among the Jurassic "aganitici" there is a certain homogeneity in the suture, mainly in the pronounced lateral lobe, and in the projected ventral saddle with its shallow lobe. The differences encountered are more a matter of degree, with some element of the suture being larger, deeper, or of slightly different shape (Fig. 14). The scope of variation is similar to that found in species of the Clydonautilidae.

The early "aganitici" such as "*Hercoglossa*" *kochi* (Prinz) of the Lias, *Nautilus subsinuatus* d'Orbigny of the Inferior Oolite, *N. crassisinuatus* Crick also of the Inferior Oolite, *N. pellerensis* Vialli of the Bajocian of north Italy, and *N. dullii* Gem-

Fig. 15. Cross sections of the conch of *A, Pseudaganides pulchellus* (Jeannet) 1951, fig. 45, diameter 44 mm.; *B, P. krenkeli* (Jeannet) 1951, fig. 37, diameter 50 mm.; *C, P. oppeli* (Zittel) 1868, pl. 4, fig. 1b, diameter 100 mm.; *D, P. subbiangulatus* (d'Orbigny) 1850, from d'Orbigny, 1843, pl. 34, fig. 2, diameter 92 mm.; *E, P. rogeri* (Loesch) 1914, fig. 3b, height 50 mm.; *F, P. schneidi* (Loesch) 1914, fig. 2a, height 35 mm.; *G, P. aganiticus* (Schlotheim) from Jeannet, 1951, fig. 42, height 25 mm.; *H, P. kochi* (Prinz) 1906, fig. 5, height 77 mm.; *I, P. frickensis* (Jeannet) 1951, fig. 36, diameter 46 mm.; *J, P. strambergensis* (Oppel) 1865, pl. 2, fig. 8a, diameter 98 mm.; *K, P. branhuberi* (Loesch) 1914, fig. 5b, height 50 mm.; living chamber; *L, P. branhuberi* (Loesch) 1914, fig. 5a, height 39 mm.; phragmocone; *M, P. sinuatus* (Sowerby) from d'Orbigny, 1843, pl. 32, diameter 188 mm.; *N, P. gravesianus* (d'Orbigny) 1843, pl. 38, diameter 270 mm.; *O, Pseudonautilus aturioides* (Pictet) 1867, pl. 11, fig. 1c, diameter 60 mm.; *P, P. malbosi* (Pictet) 1867, pl. 9, fig. 2b, diameter 100 mm.; *Q, Pseudaganides dumasi* (Pictet) 1867, pl. 10, fig. 2b, diameter 69 mm.

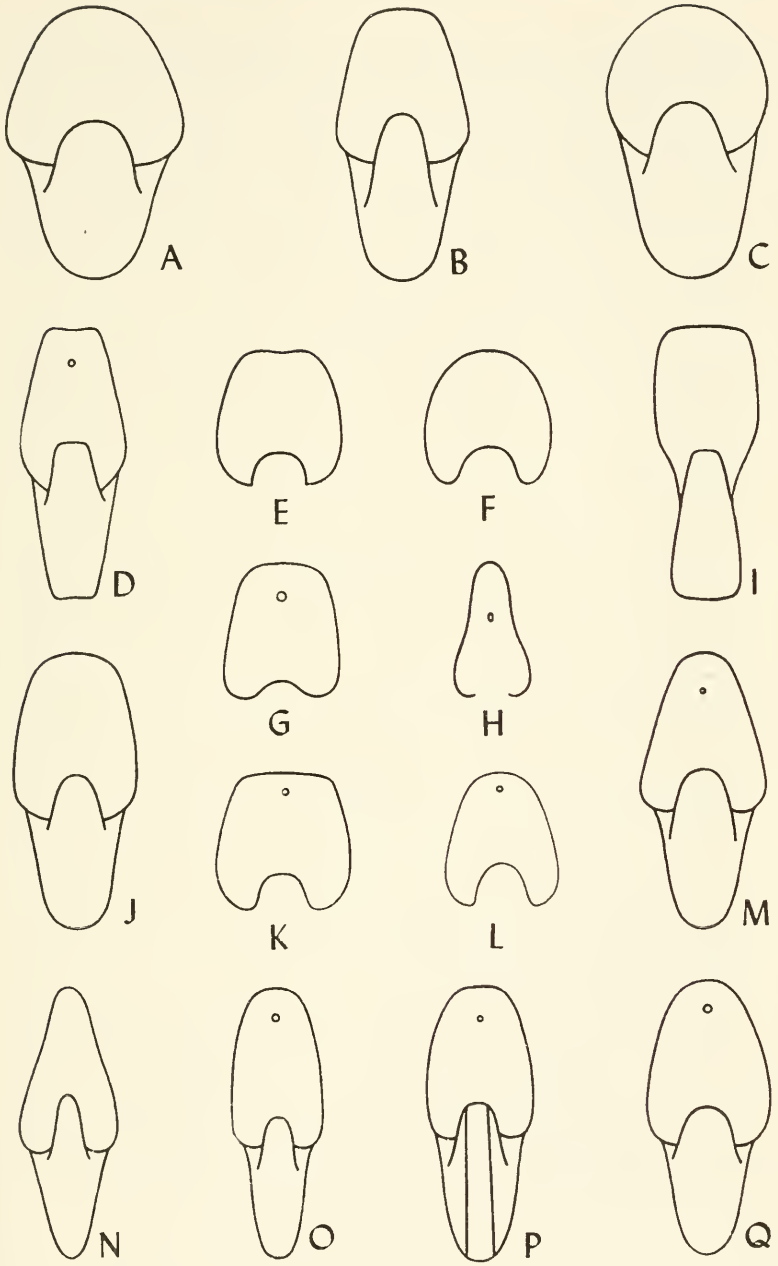

Figure 15

mellaro are all compressed, involute forms with the whorls higher than wide. The sutures have pronounced lateral lobes and are strongly projected towards the venter which they cross in nearly a straight line. In nearly all other species of *Pseudaganides* there is a slight lobe on the peripheral area. The lateral saddle in the above early "aganitici" is quite variable. It is very pronounced in *N. subsinuatus* and *N. crassisinuatus* but very low in *N. pellerensis* and *N. duilii*. In each of these latter two species the umbilical seam passes through about the middle of the lateral saddle.

The sutures in most of the remaining "aganitici" of the Jurassic have a shallow lobe on the venter. This small ventral lobe appears to persist in forms like *N. ammoni* Loesch, *N. rogeri* Loesch, *N. schneidi* Loesch, etc., but in *N. schlosseri*, after the ventral lobe having been present, it disappears in the last few sutures and is nearly straight or only slightly arched across the venter (see Loesch, 1914, p. 115, fig. 8).

There is a rather large degree of variation in the shape of the conch in the species here assigned to *Pseudaganides* (Fig. 15). All of the species have nautiliconic conchs but vary in the character of the ventral shoulders and in the width to height proportions of the whorl section. In the type species, *N. kutchensis*, the whorl section is subrectangular with subangular ventral shoulders, an arched venter, and flattened convergent flanks. Subangular to acutely rounded ventral shoulders are present in *N. argoviensis* Loesch, *N. ammoni* Loesch, *N. klebelsbergi* Loesch, *N. aganiticus* Schlotheim, *N. tubingensis* Loesch, *N. helveticus* Loesch, *N. brunhuberi* Loesch, *N. frickensis* Jeannet, and *N. subbiangulatus* d'Orbigny. Well rounded ventral shoulders and arched venters are found in *N. pulchellus* Jeannet, *N. schneidi* Loesch, *N. strambergensis* Oppel, *N. franconicus* Oppel and *N. oppeli* Zittel. Some species have slightly concave venters, as in *N. subbiangulatus* d'Orbigny and *N. rogeri* Loesch. In *N. ammoni* and *N. schlosseri* the venter becomes slightly concave on the living chamber, but is arched on the phragmocone. The width and height measurements of the whorl section in *N. kutchensis* are approximately equal. This same ratio is present in many other species of *Pseudaganides* (e.g. *N. pulchellus* Jeannet, *N. rogeri* Loesch, *N. brunhuberi* Loesch, *N. schneidi* Loesch, *N. ammoni* Loesch, etc.). More compressed species include *N.*

subbiangulatus d'Orbigny, *N. frickensis* Jeannet, *N. strambergensis* Oppel, etc. *Nautilus kochi* has a highly compressed conch with convergent whorl sides and a rather narrow rounded venter. It appears to be merely an extreme form of *Pseudaganides* and does not warrant separation as a distinct genus. *Hercoglossoceras* established by Spath for *N. kochi* is here considered a synonym of *Pseudaganides*. Whereas the degree of convergence of the whorl sides is greatest in *N. kochi* the degree of compression of the conch is found in several other species.

Loesch (1914) has described several species of Upper Jurassic nautiloids which are very similar in conch shape and suture to typical *Hercoglossa* of the late Cretaceous and early Tertiary. That is, these species have well rounded ventral shoulders and arched venters. Spath (1927a) included them tentatively in *Hercoglossa* but also expressed the opinion that they "probably form an independent development." These Upper Jurassic "hercoglossids" include among others: *N. franconicus* Oppel, *N. schneidi* Loesch, *N. rogeri* Loesch, *N. brunhuberi* Loesch, *N. roemeri* Loesch, *N. schwertschlageri* Loesch, *N. schlosseri* Loesch, *N. stromeri* Loesch, *N. oppeli* Zittel, and *N. strambergensis* Oppel. In all of these species, however, there is a shallow ventral lobe which is not found in the Upper Cretaceous-Tertiary *Hercoglossa*. The great similarity of these two groups is thought to be a case of homeomorphy. The true *Hercoglossa* develop from Cretaceous *Cimomia* whereas the Jurassic "aganitici" are derived from Liassic *Cenoceras*.

Pseudaganides is widely distributed in Jurassic strata throughout Europe, and in Pakistan. Of a total of 37 species listed below, 1 is from the Lias, 9 are from Middle Jurassic strata, and 28 are known from Upper Jurassic formations.

DISTRIBUTION OF SPECIES OF THE GENUS PSEUDAGANIDES

Species	Stratigraphic Distribution	Geographic Distribution
P. aganiticus (Schlotheim) 1820	Jurassic (Oxfordian)	France
P. ammoni (Loesch) 1914	Jurassic (Upper)	Europe
P. argoviensis (Loesch) 1912	Jurassic (Oxfordian)	Switzerland

Species	Stratigraphic Distribution	Geographic Distribution
P. bodeni (Loesch) 1914	Jurassic (Oxfordian)	France
P. brunhuberi (Loesch) 1914	Jurassic (Upper)	Europe
P. clausus (d'Orbigny) 1842	Jurassic (Bajocian)	France
P. crassisinuatus (Crick) 1898	Jurassic (Bajocian)	England
P. drepanensis (Tagliarini) 1901	Jurassic (Middle)	Sicily
P. duilii (Gemmellaro) 1886	Jurassic (Middle)	Sicily
P. franconicus (Oppel) 1865	Jurassic (Tithonian)	Europe
P. frickensis (Jeannet) 1951	Jurassic (Callovian)	Switzerland
P. girardoti (de Loriol) 1903	Jurassic (Oxfordian)	Switzerland
P. glaber (Foord and Crick) 1890	Jurassic	England, France
P. gravesianus (d'Orbigny) 1843	Jurassic	France
P. helveticus (Loesch) 1914	Jurassic (Upper)	Switzerland
P. klebelsbergi (Loesch) 1914	Jurassic (Tithonian)	Czechoslovakia
P. kochi (Prinz) 1906	Jurassic (Lias)	Austria, Hungary
P. krenkeli (Jeannet) 1951	Jurassic (Upper)	Switzerland
P. kutchensis (Waagen) 1873	Jurassic (Upper)	Pakistan
P. ledonicus (de Loriol) 1903	Jurassic (Oxfordian)	France
P. oppeli (Zittel) 1868	Jurassic (Upper)	Europe
P. pellerensis (Vialli) 1937	Jurassic (Middle)	North Italy
P. portlandicus (Foord and Crick) 1890	Jurassic (Upper)	England
P. pulchellus (Jeannet) 1951	Jurassic (Oxfordian)	Switzerland

Species	Stratigraphic Distribution	Geographic Distribution
P. roemeri (Loesch) 1914	Jurassic (Upper)	East Europe
P. rogeri (Loesch) 1914	Jurassic (Upper)	East Europe
P. rogeri (de Loriol) 1872	Jurassic (Upper)	France
P. schlosseri (Loesch) 1914	Jurassic (Tithonian)	East Europe
P. schlotheimi (Loesch) 1914	Jurassic (Middle)	Lorraine
P. schneidi (Loesch) 1914	Jurassic (Tithonian)	Europe
P. schwertschlageri (Loesch) 1912	Jurassic (Upper)	Europe
P. strambergensis (Oppel) 1865	Jurassic (Tithonian)	Czecho-slovakia
P. stromeri (Loesch) 1914	Jurassic (Tithonian)	Czecho-slovakia
P. subbiangulatus (d'Orbigny) 1850	Jurassic (Bathonian)	France
P. subsinuatus (d'Orbigny) 1850	Jurassic (Middle)	England
P. tubingensis (Loesch) 1914	Jurassic (Upper)	Germany
P. tuckeryi (Gemmellaro) 1886	Jurassic (Middle)	Sicily

Genus PSEUDONAUTILUS Meek, 1876

Pseudonautilus Meek, 1876, p. 491.
Pseudonautilus Spath, 1927a, pp. 20, 22, 26.
Pseudonautilus Miller and Collinson, 1953, pp. 293-295.
Type species. *Nautilus geinitzi* Oppel, *in* Zittel, 1868, p. 45, pl. 2, figs. 1-7 (Plate 12, figures 1, 2 and Text-Figure 16 of this report).

This genus is well characterized by the extreme "goniatitic" development of its suture. Only four species are assignable to the genus and the following diagnosis has been compiled from specimens in the M.C.Z. and the description and illustrations of these species.

Conch involute, compressed, and smooth. Whorl sides flattened, venter low and broadly arched. The ventral and umbilical shoulders are rounded. The whorl section is higher than wide.

The umbilicus is very small and deep. The suture has a deep narrow ventral lobe, a large V-shaped lateral lobe followed by a rounded saddle with a small second lateral lobe just above the umbilical seam. There is a deep pointed dorsal lobe. The siphuncle is in a subventral position.

The most diagnostic character of *Pseudonautilus* is the sinuous suture with the deep V-shaped ventral lobe. The four species assignable to *Pseudonautilus* are: *P. geinitzi* Oppel, the type species; *N. aturioides* Pictet (1867); *N. dumasi* Pictet (1867); and *N. malbosi* Pictet (1867). Loesch (1914, p. 130-131) discussed in some detail various aspects of *N. geinitzi* and *N. aturioides*. *Nautilus geinitzi* is from the Upper Jurassic (Tithonian) of Moravia, Silesia, and France, and has also been recorded from the Berriasian of Tunisia by Arnould-Saget (1953). *Nautilus aturioides* is from the zone of *Hoplites boissieri,* lowest Valanginian (Loesch, 1914, p. 131). *Nautilus malbosi* Pictet has more angular ventral shoulders than in the type species and likewise the ventral and lateral lobes are rounded rather than pointed. In respect to the suture, *N. malbosi* and *N. dumasi* are more or less intermediate forms between typical *Pseudaganides* and *N. geinitzi*, the type species of *Pseudonautilus*. The assignment of these two species to *Pseudonautilus* is open to question. *Nautilus malbosi* has been recorded from Lower Cretaceous formations in central Europe (Pictet, 1867), Algeria (Pomel, 1889), and from the Crimea (Karakasch, 1907).

One of the most remarkable cases of homeomorphy among post-Carboniferous nautiloids is the similarity of *Nautilus* (*Aganides*) *bitauniensis* Haniel from the Permian Bitauni beds (Leonardian) of Timor and *Pseudonautilus geinitzi* Oppel (Fig. 16.) Miller and Collinson (1953) have recently discussed this problem and erected the genus *Permoceras* and the family Permoceratidae for Haniel's species. They likewise recognized the homeomorphous relationship of these two nautiloids. Among Triassic nautiloids sinuous sutures are found in the Clydonautilidae, Gonionautilidae Siberionautilidae, and in the genus *Clymenonautilus* of the Syringonautilidae. Sinuous sutures are, however, not common in Permian nautiloids. Among the forms comprising the Grypoceratidae, *Grypoceras* (*Plummeroceras*) *plummeri* (*Kummel*, 1953c) — a compressed evolute, quadrate whorled form — has a suture with a deep ventral lobe and a broad

deep lateral lobe. The general shape of the conch except for the degree of involution is rather similar in *G.* (*Plummeroceras*) and *Permoceras*. Within the complex of Permian nautiloids now known it seems more logical to consider *Permoceras* an offshoot of the *Domatoceras-Grypoceras* evolving stock and thus a member of the Grypoceratidae.

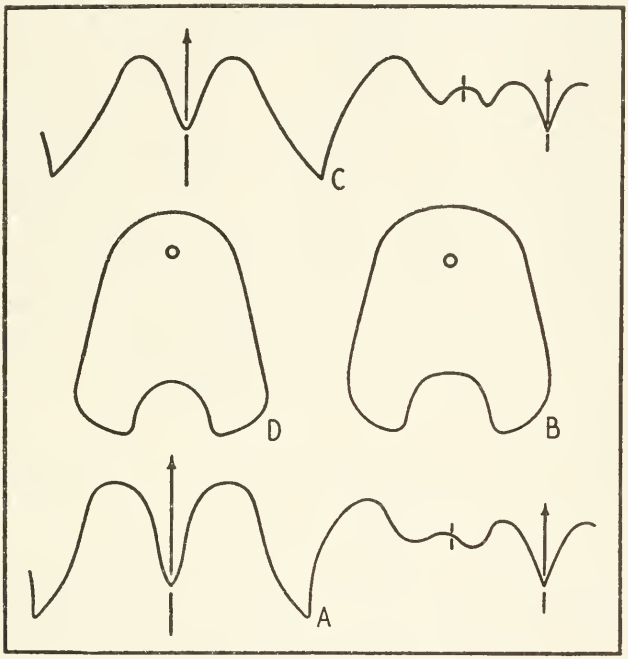

Fig. 16. Diagrammatic representation of sutures and cross sections of *Permoceras bitauniense* (Haniel) *A*, *B*, and *Pseudonautilus geinitzi* (Oppel) *C*, *D*, all X 1. From Miller and Collinson, 1953, fig. 1.

Subfamily PARACENOCERATINAE Spath, 1927

When Spath established this taxonomic unit (originally as a family) he included in it *Paracenoceras* Spath, *Tithonoceras* Retowski, *Somalinautilus* Spath, *Aulaconautilus* Spath, *Carinonautilus* Spengler and with question *Heminautilus* Spath. Ex-

amination of topotypes of *Heminautilus etheringtoni* Durham and the descriptions and illustrations of *H. lallierianus* d'Orbigny (especially in Douvillé, 1916, pl. 17) lead me to conclude that these species belong more properly in the Cymatoceratinae. They have the characteristic ribbing, even though in some specimens the ribbing is very weak or absent, and a hercoglossid suture, more sinuous than the suture in most species of the Paracenoceratinae. However, on the basis of the ornament alone this genus should not be left in the Paracenoceratinae.

Carinonautilus is a monotypic form known only from the Upper Cretaceous of south India. The paracenoceratids are primarily a Jurassic radiation from the *Cenoceras* complex and it is difficult to visualize a derivation of *Carinonautilus* from this source. It is here allied to the Nautilinae and considered a derivative of *Eutrephoceras* which is the long-persisting, slowly-evolving stock ranging from the Upper Jurassic to the middle Tertiary. Of the remaining genera, only *Paracenoceras* is widespread and fairly common as far as Mesozoic nautiloids go. It has by far the largest number of species; of a total of 42 species in this family 35 belong in *Paracenoceras*. *Tithonoceras* is monotypic, *Somalinautilus* and *Aulaconautilus* have three or less species each.

Whereas Spath did not diagnose this family at length, he did state that it was "characterized by differentiation of the periphery, generally associated with increase of the sinuosity of the suture line, and a ventral lobe" (Spath, 1927a, p. 25). *Paracenoceras* has a broad, generally sulcate periphery. *Tithonoceras* has a broad flattened periphery with a median furrow and the ventrolateral area projected into a prominent blunt keel aligned by furrows. *Somalinautilus* has an arched venter with angular ventral shoulders. *Aulaconautilus* has longitudinal ribs on the peripheral area.

Both *Paracenoceras* and *Somalinautilus* are interpreted as offshoots from the *Cenoceras* complex. Both of these genera first appear in the Middle Jurassic and it seems likely that they stem from separate sources within *Cenoceras*. *Aulaconautilus* and *Tithonoceras* are more specialized developments stemming from *Paracenoceras*. The subfamily is largely confined to the eastern hemisphere, being known from England, Europe, east and north Africa, Arabia, and Pakistan. The only occurence of a member

Fig. 17. Geographic distribution of species of the subfamily Paracenoceratinae in formations of Jurassic and early Cretaceous age.

of this subfamily in the western hemisphere is *Paracenoceras* in Cuba. As is so characteristic of post-Triassic nautiloids the main stock of a subfamily is generally a highly variable form with many described species and a wide geographic distribution. This is well illustrated in the distribution of species of this subfamily (Fig. 17).

Genus PARACENOCERAS Spath, 1927

Paracenoceras Spath, 1927a, pp. 22, 25.
Paracenoceras Spath, 1935b, pp. 224-225.
Paracenoceras Scott, 1943, pp. 88, 89.
Nautilus (*Paracenoceras*) Jeannet, 1951, pp. 10-17.
Paracenoceras Miller and Collinson, 1952, pp. 626-628.
Type species. Nautilus hexagonus J. de C. Sowerby, 1826, pl. 529, fig. 2 (illustrated here on Plate 8, fig. 1, and Plate 13, figs. 1, 2; Text Fig. 18). Type by original designation.

Paracenoceras is the only genus of the Paracenoceratinae that is nearly world wide in distribution and includes a relatively large number of species. Of the remaining genera of this subfamily one is monotypic and the remaining two genera contain no more than three species apiece. The type species — *Nautilus hexagonus* J. de C. Sowerby — was previously only known through the rather unsatisfactory description and woodcut illustration (J. de C. Sowerby, 1826, pl. 529, fig. 2). Sowerby's type is illustrated on Plate 13, figures 1, 2, and Plate 8, figure 1 and Text Figure 18.

The genus can be diagnosed as follows: Conch robust, involute, smooth. Whorl section subtrapezoidal in outline. Whorl sides flattened, convergent towards a broad venter that may be flattened or truncate to distinctly sulcate. Ventral shoulders well rounded. Umbilicus generally small, umbilical shoulders rounded, umbilical walls steep. The shell is smooth except for sinuous growth lines which form a deep sinus on the broad venter. The suture is only slightly sinuous but with a distinct ventral and lateral lobe and a small saddle at the umbilical shoulder and wall. The position of the siphuncle is quite variable but never in an extreme ventral or dorsal position. The polished median section of Sowerby's type specimen shows that the siphuncle is beaded and with short funnels (Plate 8, fig. 1). Similar beaded siphuncles have been also noted by Spath (1927a,

p. 23) in species of "*Bisiphytes*," "*Digonioceras*," and *Cymatoceras*.

Approximately 35 species of *Paracenoceras* have been recorded most of which are from Upper Jurassic strata. Spath (1935b, p. 224) has described *Paracenoceras prohexagonum* from strata of

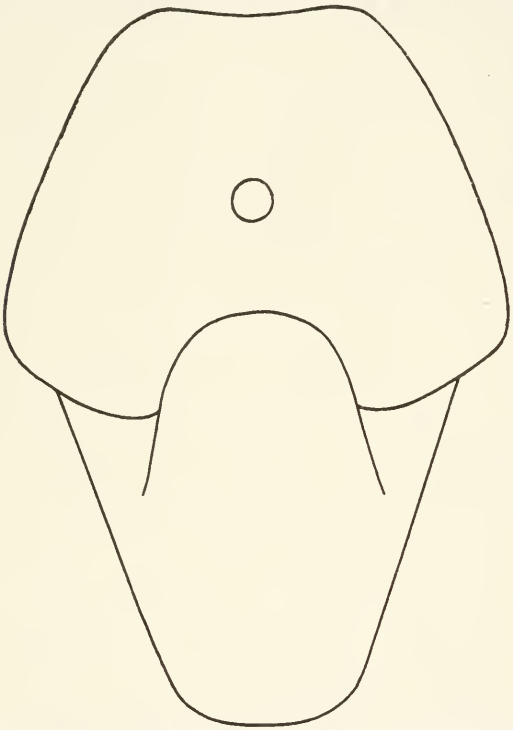

Fig. 18. *Paracenoceras hexagonum* (Sowerby). Diagrammatic cross section of holotype represented by figures 1, 2, Plate 13, and figure 1, Plate 8, X 1.

Bathonian? age. This is the oldest species known, and the youngest species of *Paracenoceras* appears to be *P. rhodani* (Roux) from the Albian of Switzerland.

Sowerby's type of *Nautilus hexagonus*, refigured here on Plate 13, figures 1, 2 and Text Figure 18, is a large phragmocone measuring 95 mm. in diameter, 54 mm. in height of last whorl, and 67 mm. in width of the last whorl. The whorl sides are only slightly convex and converge towards a broad sulcate venter.

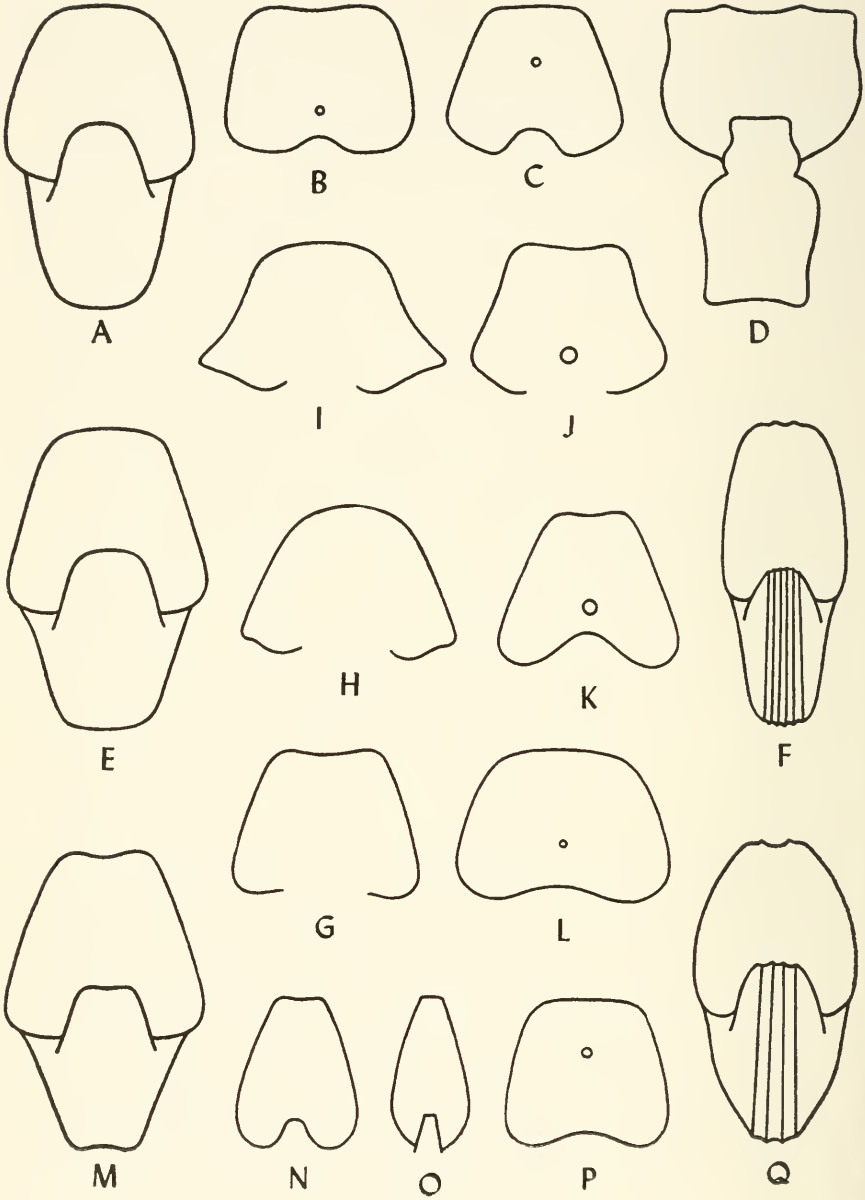

Figure 19

The umbilical and ventral shoulders are well rounded. The umbilicus is fairly large, deep, and funnel shaped. The umbilical walls are very steep. The large siphuncle is subcentral in position.

There is much variation in shape of the whorl section among the various species of *Paracenoceras*. The cross sections of 12 species are illustrated in Figure 19 to show the degree of variation. Sulcation of the venter of the adoral volution as on the type species, is not present on several of the species which have merely truncated venters or ventral areas slightly arched. *Paracenoceras marocense* Miller and Collinson (1952) has a broad sulcate venter at early maturity but the venter becomes arched with increasing size (Text Figure 19 *G-I*). The whorl sides also show some variation from being slightly concave as in *P. hexagonum* and *P. marocense*, to flattened or slightly convex in most of the remaining species. Variations in suture are mostly a matter of degree. Sutures of several species of *Paracenoceras* are illustrated in Figure 20 for comparison.

Paracenoceras costatum Scott (1943, p. 88, pl. 24, figs. 1, 3), with prominent sigmoidal costae on the whorl sides, belongs in the genus *Procymatoceras*. Scott (1943, p. 89) compared "*Paracenoceras*" *costatum* with P. *jumarense* (Waagen, 1873, p. 21, pl. 4, figs. 1a, b) which has sigmoidal ribs only on the whorl sides, that terminate in large tubercles at the ventrolateral shoulder. However, Spath (1927a, p. 32) questions the accuracy of

Fig. 19. Cross sections of the conch of *A, Paracenoceras callovicnsis* (Oppel), from Waagen 1873, pl. 3, fig. 2b, diameter 65 mm.; *B. P. subhexagonum* Jeannet 1951, fig. 19, height 42 mm.; *C, P. rollieri* (Loesch) from Jeannet 1951, fig. 29, height 27 mm.; *D, Aulaconautilus bicarinatus* Jeannet 1951, fig. 32, diameter 41 mm.; *E, Paracenoceras wandaensis* (Waagen) 1873, pl. 4, fig. 3b, diameter 85 mm.; *F, Aulaconautilus sexcarinatus* (Pictet) 1867, pl. 10, fig. 1b, diameter 107 mm., the genotype of *Aulaconautilus; G, H, I, Paracenoceras marocense* Miller and Collinson, 1952, fig. 1 (*G*, height 28 mm.; *H*, height 48 mm.; *I*, height, 72 mm.); *J, P. prohexagonum* Spath 1935, fig. 46, height 44 mm.; *K, P. hexagonum* (Sowerby) from Spath 1935, fig. 4d, height 56 mm., the genotype of *Paracenoceras; L, P. dilatatus* Jeannet 1951, fig. 8, height 140 mm.; *M, P. kumagunensis* (Waagen) 1873, pl. 3, fig. 1b, diameter 72 mm.; *N, P. herznachensis* Jeannet 1951, fig. 14, height 100 mm.; *O, P. ennianum* (Dacqué), from Scott 1940, pl. 24, fig. 2, height 70 mm.; *P, P. arduennensis* (Loesch, 1914) from Jeannet 1951, fig. 26, height 19 mm.; *Q, Aulaconautilus picteti* (Oppel), from Zittel 1868, pl. 3, fig. 3b, diameter 95 mm.

Waagen's illustration and points out that the specimens are badly weathered. Spath quite rightly maintains that the affinities of *P. jumarense* are very doubtful and the species can be retained in *Paracenoceras* with question.

A list of the species assigned to *Paracenoceras* with their generalized geologic and geographic data is given below. Most of the species are from the Jurassic Tethyian geosynclinal area and adjoining epicontinental seas of Europe. Several occurrences

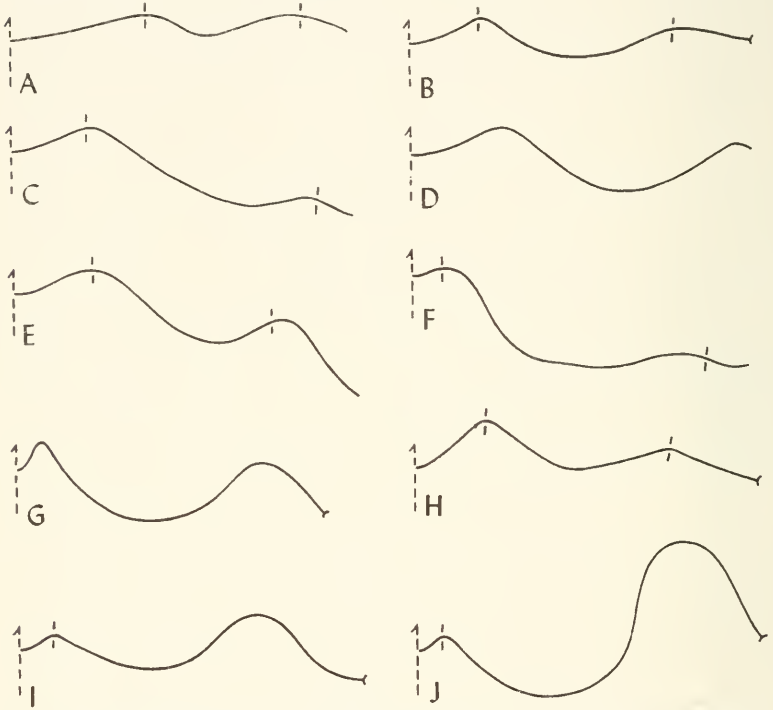

Fig. 20. Diagrammatic representation of sutures of *A*, *Paracenoceras dilatatus* Jeannet 1951, fig. 8; *B*, *P. hexagonum* (Sowerby), from Spath 1935, fig. 4e, the genotype of *Paracenoceras*; *C*, *P. acklini* Jeannet 1951, fig. 25; *D*, *P. marocense* Miller and Collinson 1952, fig. 1A; *E*, *P. rollieri* (Loesch, 1914) from Jeannet 1951, fig. 29; *F*, *P. herznachensis* Jeannet 1951, fig. 14; *G*, *Heminautilus stantoni* Scott 1940, fig. 179; *H*, *Paracenoceras prohexagonum* Spath 1935, fig. 4c; *I*, *Heminautilus etheringtoni* Durham 1946, fig. 3C; *J*, *Heminautilus lallierianus* (d'Orbigny) from Durham, 1946, fig. 3A. All figures greatly reduced.

in eastern Africa, Madagascar, Arabia, and in Pakistan form an eastern extension of the European faunal distribution. The only occurrence known in the Western Hemisphere is in Cuba (Sánchez Roig, 1951). As noted above, most of the species of *Paracenoceras* are Upper Jurassic in age.

DISTRIBUTION OF SPECIES OF THE GENUS PARACENOCERAS

Species	Stratigraphic Distribution	Geographic Distribution
P. acklini (Jeannet) 1951	Jurassic (Callovian)	Switzerland
P. arduennensis (Loesch) 1914	Jurassic (Oxfordian)	France
P. bruntrutanae (Kuhn) 1936	Jurassic (Upper)	Germany
P. calloviensis (Oppel) 1858	Jurassic (Callovian)	Europe
P. dilatatus (Jeannet) 1951	Jurassic (Callovian)	Switzerland
P. divesianus (Kuhn) 1936	Jurassic (Upper)	France
P. dorsatus (Roemer) 1836	Jurassic (Upper)	Germany
P. dorsoexcavatum (Parona and Bonarelli) 1897	Jurassic (Callovian)	France
P. ennianum (Dacqué) 1905	Jurassic (Upper)	Somaliland
P. giganteus (d'Orbigny) 1825	Jurassic (Upper)	France
P. granulosum (d'Orbigny) 1843	Jurassic (Upper)	France
P. herznachensis Jeannet, 1951	Jurassic (Callovian)	Switzerland
P. hexagonoides Spath, 1927	Jurassic (Tithonian)	Pakistan
P. hexagonum (J. de Sowerby) 1826	Jurassic (Upper)	Europe
P. jeanneti Sanchez Roig, 1951	Jurassic (Oxfordian)	Cuba
P.? jumarense (Waagen) 1873	Jurassic (Bathonian)	Pakistan

Species	Stratigraphic Distribution	Geographic Distribution
P. kumagunense (Waagen) 1873	Jurassic (Callovian)	Pakistan
P. latifrons (Zwierzycki) 1914	Jurassic (Upper)	Tanganyika
P. marocense Miller and Collinson, 1952	Jurassic (Upper)?	Morocco
P. mjatschkowanus (Loesch) 1914	Jurassic (Upper)	Russia
P. morcaui (d'Orbigny) 1842	Jurassic (Kimmeridgian)	France
P. mullerriedi Sanchez Roig, 1951	Jurassic (Oxfordian)	Cuba
P. prohexagonum Spath, 1935	Jurassic (Bathonian?)	British Somaliland
P. rhodani (Roux) 1848	Cretaceous (Albian)	Switzerland
P. rollieri (Loesch) 1914	Jurassic (Oxfordian)	Switzerland
P. sattleri (Krenkel) 1910	Jurassic (Kimmeridgian)	Tanganyika
P. schattenbergi (Kuhn) 1936	Jurassic (Upper)	Germany
P. schusteri (Loesch) 1912	Jurassic (Kimmeridgian)	France
P. siculus (Gemmellaro) 1868	Jurassic (Upper)	Sicily
P. sinuosus (Roemer) 1836	Jurassic (Upper)	Germany
P. staffelbergensis (Kuhn) 1936	Jurassic (Upper)	Germany
P. subhexagonus (Jeannet) 1951	Jurassic (Callovian)	Switzerland
P. volgensis (Nikitin) 1888	Jurassic	Russia
P. wandaense (Waagen) 1873	Jurassic (Upper)	Pakistan
P. wilmae (Jeannet) 1951	Jurassic (Callovian)	Switzerland

Genus AULACONAUTILUS Spath, 1927

Aulaconautilus Spath, 1927a, pp. 22, 25.

Nautilus (*Aulaconautilus*) Jeannet, 1951, p. 17.

Type species. Nautilus sexcarinatus Pictet, 1867, Pl. 10, figs. 1a-c (reproduced here as Plate 14, figs. 1, 2). Type by original designation.

The following diagnosis is made from study of the descriptions and illustrations of the three species that can be assigned to this genus. No specimens were available for study. Conch involute, generally compressed, with greatest width of the whorls just below the umbilical shoulders. Whorl sides smooth, convex and converging. Ventral shoulders rounded, venter broad, low, and with longitudinal ribs. Umbilicus very small, umbilical shoulders rounded. Suture sinuous with a shallow ventral lobe, a broad deep lateral lobe with a saddle at the umbilical shoulder. Position of the siphuncle not known.

Only three species can be placed in *Aulaconautilus;* these are *A. sexcarinatus* (Pictet) the type species, *A. pictcti* (Oppel), and *A. bicarinatus* (Jeannet). There is variability in the conch shape, suture, and ornamentation. The type species, *A. sexcarinatus,* has eight longitudinal ribs on the venter (Plate 14, figs. 1, 2 and Text Figure 19*F*), divided by shallow furrows. The median furrow is the most prominent. The ribs at the ventrolateral edge are the weakest of the ribs on the venter. *Aulaconautilus pictcti* has only four longitudinal ribs all of equal prominence; the median furrow is the widest and deepest of the furrows between these ribs. This species likewise is much more inflated than the type species (Text Fig. 19*Q*). *Aulaconautilus bicarinatus* has a more depressed, subquadratic whorl section with a broad flattened venter. There are four widely spaced longitudinal ribs on the venter (Text Fig. 19*D*). The ornamentational pattern of longitudinal ribs on the venter, which characterizes *Aulaconautilus,* is unique for post-Triassic nautiloids. A homeomorphous development is the Permian and Triassic genus *Aulametacoceras* Miller and Unklesbay. The type of this genus is Middle Permian in age (from Arizona). The only other species assigned to it is *Nautilus rectangularis* Hauer of Upper Triassic age. *Aulametacoceras* is considered a radiation from the stable evolving *Metacoceras* complex (Kummel, 1953c).

The sutures of species of this genus, especially those of the

type species, are very similar in plan and degree of sinuosity to those of *Pseudaganides*. The other groups of the Paracenoceratinae have sutures with very shallow lobes and saddles.

The three known species of *Aulaconautilus* come from Upper Jurassic strata of Europe.

Genus TITHONOCERAS Retowski, 1894

Tithonoceras Retowski, 1894, p. 223.
Tithonoceras Crick, 1908, p. 14.
Tithonoceras Spath, 1927a, pp. 20, 22, 25.
Type species. Tithonoceras zitteli Retowski, 1894, p. 223, pl. 13, figs. 2a, b, c (refigured here on Plate 15, figs. 1, 2).

This is another of the numerous monotypic Mesozoic nautiloid genera. The type species is from Tithonian (Upper Jurassic) strata of the Crimea. The conch is evolute, compressed, and smooth. The whorls are subrectangular in outline, being higher than wide. The venter is broad, flattened, and with a shallow median furrow. The ventral shoulders are inflated and form a smooth keel-like ridge that is aligned on the venter and the whorl sides by a furrow. The ventral furrow aligning the ventrolateral keel is rather narrow but very distinct. The furrow on the whorl sides adjoining the ventrolateral keel is concave and broad occupying nearly half of the whorl side. The dorsal half of the whorl side is convex passing onto a broadly rounded umbilical shoulder. The umbilicus is large, measuring one-eighth the diameter of the conch. The shell is smooth except for sinuous growth lines which are deeply concave on the venter. The suture is very sinuous with ventral and lateral lobes. The position of the siphuncle is not known.

Proper evaluation of monotypic forms is not entirely satisfactory. Little can be said of *Tithonoceras* except that it appears to be a specialized offshoot of *Paracenoceras*. The general conch form is unique among Carboniferous to Recent nautiloids. There are no homeomorphous types of other ages known to me. In its derivation from *Paracenoceras* there was merely greater compression of the conch and further elaboration of the ventral area.

The type and only known species of *Tithonoceras* came from Tithonian strata (Upper Jurassic) of the Crimea, Russia.

Genus SOMALINAUTILUS Spath, 1927

Type species. *Nautilus antiquus* Dacqué, 1910 (=*N. bisulcatus* Dacqué, 1905, p. 144, pl. 16, figs. 3a, b). Type by original designation. Type figure reproduced here on Plate 14, figs. 3, 4.

The Paracenoceratinae are derived from Liassic cenoceratids and are characterized by modified venters. The earliest species of this subfamily are included in the genus *Somalinautilus*. At this date only three species of *Somalinautilus* have been recorded. The type species is from Upper Jurassic (Kimmeridgian) strata of Somaliland. The other species definitely assigned to this genus are *Nautilus fuscus* Crick (1898, p. 122) and *N. clausus in* Foord and Crick (1890b, p. 284) *non* d'Orbigny (1842, p. 158, pl. 33).

From the description and illustration of the type species and study of several specimens of *Nautilus fuscus* in the British Museum (Natural History), the following diagnosis is made. Conch involute, depressed, rapidly expanding, whorls wider than high. Venter slightly arched with subangular ventral shoulders, with a distinct furrow on venter adjoining the ventral shoulder. The whorl sides are concave adjacent to the ventral shoulders and convex towards the umbilicus. Umbilical shoulders are sharply rounded and the umbilical wall very steep. Umbilicus measures less than one-quarter the diameter of the conch. Surface of the conch with sinuous growth lines and may or may not have longitudinal striae. Suture forms shallow ventral lobe, generally an angular saddle at the ventral shoulder followed by a broad, shallow, lateral lobe, with a low saddle on the umbilical wall. The position of the siphuncle in the type species is not known but in *Nautilus fuscus* it is slightly below the center.

Each of the generic groups of the Paracenoceratinae is very distinct and *Somalinautilus* with its subangular ventral shoulders and low arched venter is readily differentiated from the other genera. *Somalinautilus* most probably arose directly out of the *Cenoceras* complex and not from *Paracenoceras*. There are several quadrate whorled forms of *Cenoceras* which could have given rise to those Middle and Upper Jurassic species placed in *Somalinautilus*. Species of this genus are known from England, France, and Somaliland.

Subfamily CYMATOCERATINAE Spath, 1927

This subfamily now comprises 10 genera of post-Triassic nautiloids which have variable conch shapes and degree of sinuosity of the suture but have in common an ornamentational pattern consisting of ribs. Ornamentation is relatively rare in post-Triassic nautiloids, excepting those forms within the Cymatoceratinae. There are no species with nodose ornamentation known. Within this subfamily there is displayed a wide range of adaptive radiation as seen in the extent of variation in conch shape and suture. The genus *Cymatoceras* is the basic adaptive type; it has an involute, rounded conch with only a slightly sinuous suture. *Paracymatoceras* is like *Cymatoceras* in conch form but has a more sinuous suture with distinct lobes and saddles. *Syrionautilus*, *Anglonautilus*, and *Eucymatoceras* are differentiated on modifications of the ribbing plan. *Cymatonautilus*, *Heminautilus*, *Epicymatoceras* (n. gen., p. 439), and *Deltocymatoceras* (n. gen. p. 438) are differentiated by their modified conch shapes. *Heminautilus* and *Epicymatoceras* have highly compressed conchs and flattened venters. The former is very involute and the whorl section more convergent in plan. The latter is more evolute and with a simple, only slightly sinuous, suture. *Deltocymatoceras* has a subtriangular whorl section and *Cymatonautilus* has an evolute conch with a concave venter and whorl sides.

The only common and geographically-widely-distributed genus is *Cymatoceras*. This fact is clearly expressed in the number of species belonging to each group.

Cymatoceras	64 species
Paracymatoceras	6 species
Heminautilus	5 species
Procymatoceras	4 species
Eucymatoceras	3 species
Anglonautilus	3 species
Cymatonautilus	2 species
Syrionautilus	1 species
Epicymatoceras	1 species
Deltocymatoceras	1 species

Cymatoceras has a truly world-wide distribution. The other genera are largely confined to Europe in the epicontinental seas

adjoining the Tethyian geosyncline (Text-Figs. 21, 22). *Eucymatoceras, Anglonautilus, Syrionautilus, Cymatonautilus, Epicymatoceras,* and *Deltocymatoceras* are known only from a belt extending from England to the Crimea or Caucasus Mountains in Russia in sediments of the Jurassic and Cretaceous epicontinental seas of and adjoining the Tethys proper. *Procymatoceras* is known from England, Pakistan, and Ethiopia; *Heminautilus* and *Paracymatoceras* are known outside the European Tethyian belt from North and South America, Ethiopia, and Japan.

The known distribution of fossil nautiloids is so dependent on factors of preservation and concentration of field collecting that it is probably dangerous to make any too-sweeping conclusions. However, the number of species does at least reflect the relative abundance of the various genera. If we think of the Tethys as an ancient circum-equatorial sea the Cymatoceratinae are found to be largely confined to the borders of this seaway. Many genera (e.g. *Eucymatoceras, Syrionautilus, Cymatonautilus, Epicymatoceras,* and *Deltocymatoceras*) are confined entirely to the European-Middle East portions of this circum-equatorial sea.

Analysis of the distribution of the Cymatoceratinae on a time basis throws some light on the general problem of their evolution. *Procymatoceras* and *Cymatonautilus* are known only from Middle and Upper Jurassic strata. The species of these genera are confined to the marginal seaways of the Tethys from England to India. Whereas, to the best of my knowledge, the species of these two genera have never been found in a single stratum and locality, their geographic and time ranges do overlap.

In the Cretaceous, the genus *Cymatoceras* is widely distributed throughout the period. *Anglonautilus, Eucymatoceras,* and *Heminautilus* are confined to the Lower Cretaceous. *Anglonautilus* and *Eucymatoceras* have approximately the same geographic range from England to the Black Sea. Whereas *Heminautilus* also occurs in this European-Mediterranean-belt it is likewise known from Ethiopia, Arkansas (U.S.A.), and Colombia. The Upper Cretaceous genera *Epicymatoceras* and *Deltocymatoceras* occur together in the type Maestrichtian area of Belgium, and *Syrionautilus* is confined to the Middle East.

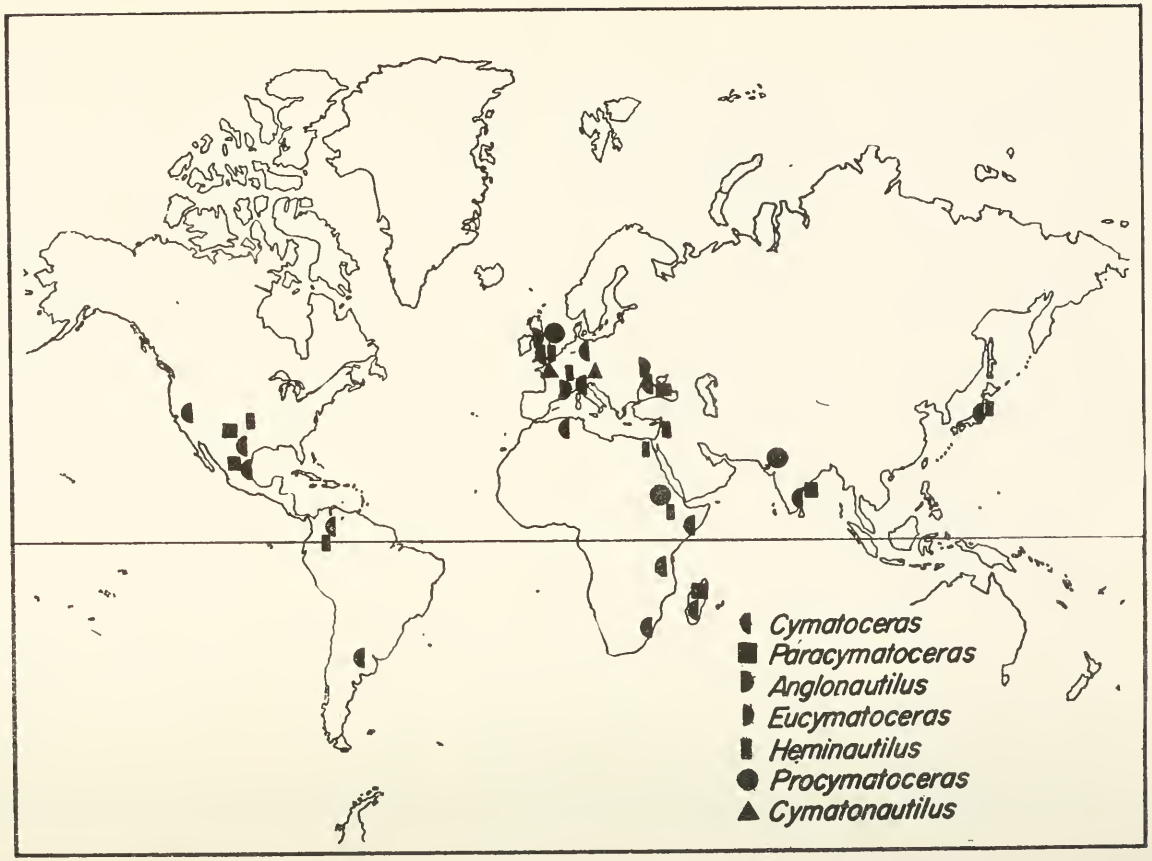

Fig. 21. Geographic distribution of species of the subramily Cymatoceratinae in formations of Lower Cretaceous age.

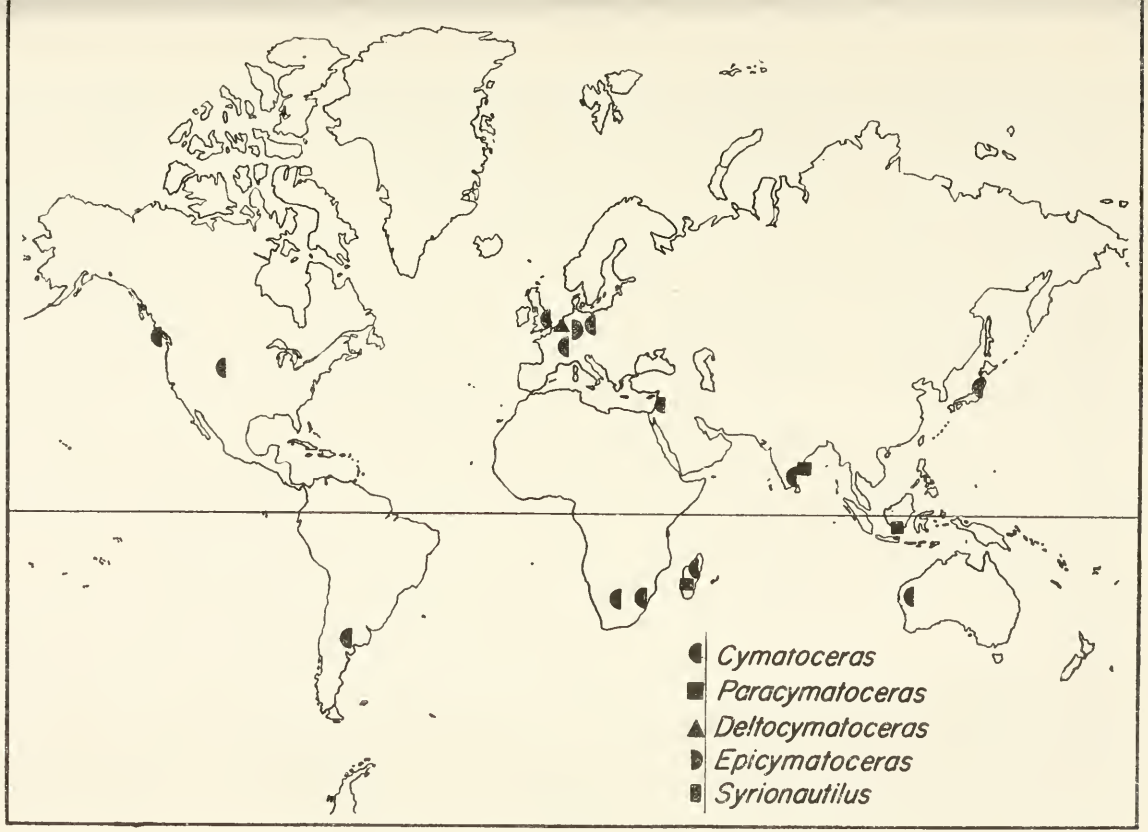

Fig. 22. Geographic distribution of species of the subfamily Cymatoceratinae in formations of Upper Cretaceous age.

The wide range in variation of conch shape and suture within the Cymatoceratinae produced many homeomorphs to other members of the Nautilidae. The presence of the characteristic ribbing makes differentiation easy. The conch shape and suture of *Deltocymatoceras* are closely similar to that of *Angulithes* of the Hercoglossinae. The conch shape and suture of many species of *Cymatoceras* and *Eucymatoceras* are nearly the same as that found in many species of *Eutrephoceras* and *Cimomia*. The suture of *Paracymatoceras* is identical in plan with that found in *Hercoglossa*.

This great variability in conch shape and suture leads me to believe that the Cymatoceratinae form a phyletic group which has as its main genetic base the ribbing character. Once established, this genetic line had its own adaptive radiation which is expressed in the many conch shapes, rib patterns, and sutures as it is in any other group of Mesozoic nautiloids. This subfamily is the dominant group of Cretaceous nautiloids. Ribbing, on a pattern somewhat like that in the Cymatoceratinae, occurred only once before, and that was in a single species of Upper Triassic nautiloid-*Proclydonautilus spirolobus* (Dittmar). The ribbing in this species is very fine and like that in *Syrionautilus*, whereas in most other genera and species of the Cymatoceratinae the ribbing is coarser. It is important to note that *Proclydonautilus spirolobus* belongs to a family that characteristically has smooth conchs except for a few forms with nodes developed during some stage of their ontogeny (*Cosmonautilus* Hyatt and Smith, 1905, and *Callaionautilus* Kieslinger, 1924). The ribbing patterns found in species of *Pleuronautilus* are quite different from those of the Cymatoceratinae.

Data are insufficient to decipher precisely the evolutionary lines within the Cymatoceratinae. The evidence available seems to point to *Cymatoceras* as the parent stock which gave rise to most of the remaining adaptive types. The origin of the subfamily must be directly or indirectly among the cenoceratid complex of the Lower and Middle Jurassic. Even though *Cymatonautilus* and *Procymatoceras* are the oldest forms known, they are both rather specialized and probably not ancestral to *Cymatoceras*, which as far as we now know first appears in the Cretaceous.

Neocymatoceras Kobayashi (1954) was established for a single

specimen from the Oligocene of Kyushu, Japan. *Neocymatoceras tsukushiense,* the type species, is a typical cymatoceratid in conch shape and rib pattern but has a strongly projected suture which forms a rounded ventral saddle, a broad sweeping lobe occupying nearly the whole whorl side, and with what appears to be the beginning of a saddle on the umbilical area. Cymatoceratids with sinuous sutures characterize *Paracymatoceras.* However, in that genus the saddles and lobes are well defined; that is, there is always a well-defined saddle on or near the umbilical shoulder. It is also true though that *Paracymatoceras* is gradational with *Cymatoceras* in regard to sutures. Those cymatoceratids with more sinuous sutures show the sutures to be more strongly projected on the ventral area and in this way give the sinuosity; the lateral saddle at the umbilical area is usually very weak. *Cymatoceras pseudonegama* Spengler (Fig. 24 *C*) and *C. semilobatus* Spengler (Fig. 24 *D*) have such strongly projected sutures on the umbilical area but not quite to the extent found in the Japanese Oligocene species. Similar strongly projected sutures in very small juvenile specimens of *Cymatoceras* have been described and figured by Kummel (1953a) from Lower Cretaceous formations of Texas. However, the suture of *Neocymatoceras tsukushiense* appears to me to lie within the range of variation of the suture of *Cymatoceras,* and the lack of any lateral saddle in the umbilical area disallows any affinity with *Paracymatoceras.* The distinctness of the suture in *Neocymatoceras tsukushiense* is only in the marked projection on the peripheral area, a modification present in several Cretaceous species. This interpretation places the Japanese species in the genus *Cymatoceras,* and *Neocymatoceras* is considered a synonym of *Cymatoceras.* It should be emphasized that *C. tsukushiense* is the only Tertiary Cymatoceratinae known.

Genus CYMATOCERAS Hyatt, 1884

Cymatoceras Hyatt, 1884, p. 301.
Cymatoceras Hyatt, 1894, p. 553.
Nautilus (Cymatoceras) Spengler, 1910, p. 127.
Cymatoceras Spath, 1927a, pp. 21, 25.
Cymatoceras Miller and Harris, 1945, p. 2.
Cymatoceras Durham, 1946, p. 429.
Neocymatoceras Kobayashi, 1954a, pp. 18-20.

Type species. Nautilus pseudoelegans d'Orbigny, 1840, p. 70, pl. 8 (by original designation).

Species of *Cymatoceras* are the most common and widely distributed nautiloids of the Cretaceous. The characteristic pattern of ribbing and the slightly sinuous septa make identification of the genus easy. A cast of the type specimen (which is in the Museum of Natural History, Paris) is illustrated on Plate 16, figures 1, 2. This same specimen has previously been illustrated by Foord and Crick (1890a, p. 551, figs. 3a, b), and this same figure was reproduced in Foord's second Catalogue of the Fossil Cephalopoda in the British Museum (Foord, 1891, p. 255, fig. 59 a, b). Foord and Crick (1890a, p. 552) quote a letter from Dr. Paul Fischer expressing doubt as to the identity of d'Orbigny's type specimen. Fischer states: "The type of *Nautilus pseudoelegans* is difficult to recognize. According to the dimensions given in the original diagnosis (diameter 240 millimètres, thickness 160 mm. Paléont. Franc. p. 60) our specimens, No. 4834D, which were sent to you are typical. [Foord and Crick, page 552, state that two specimens were sent, both numbered 4834 D; the larger one is represented by their figure 3.] Moreover, they come from the neighborhood of Vandeuvre

Fig. 23. Cross sections of the conch of *A, Cymatoceras elegans* (J Sowerby) from d'Orbigny, 1840, pl. 19, fig. 2, diameter 190 mm.; *B, C. sharpei* (Schlüter) 1876; pl. 46, fig. 6, diameter 168 mm.; *C, C. tourtiae* (Schlüter) 1876, pl. 46, fig. 2, diameter 88 mm.; *D, C. cenomanensis* (Schlüter), 1876, pl. 45, fig. 2, diameter 115 mm.; *E, Procymatoceras subtruncatus* (Morris and Lycett) 1850, pl. 1, fig. 22, diameter 72 mm., the genotype of *Procymatoceras; F, Procymatoceras baberi* (Morris and Lycett) 1850, pl. 1, fig. 1a, diameter 82 mm.; *G, Paracymatoceras asper* (Oppel) from Zittel, 1868, pl. 3, fig. 1a, diameter 83 mm., the genotype of *Paracymatoceras; H, Procymatoceras? intumescens* (Waagen) 1873, pl. 3, fig. 3, diameter 90 mm.; *I, C. radiatus* (Sowerby) from d'Orbigny, 1840, pl. 14, fig. 2, diameter 188 mm.; *J, C. neocomiensis* (d'Orbigny) 1840, pl. 11, fig. 2, diameter 192 mm.; *K, C. deslongchampsianum* (d'Orbigny) 1840, pl. 20, fig. 2, diameter 65 mm.; *L. Eucymatoceras requienianus* (d'Orbigny) 1840, pl. 10, fig. 2, diameter 280 mm. (=*N. plicatus* Fitton, 1835); *M, Cymatoceras neckerianus* Pictet, 1859, pl. 16, fig. 1b, diameter 93 mm.; *N, Deltocymatoceras rugatus* (Fritsch and Schlönbach) 1872, pl. 15, fig. 2, height 80 mm.; *O, Epicymatoceras vaelsensis* Binckhorst, 1861, pl. 5c, fig. 2b, diameter 105 mm.; *P, Cymatoceras albensis* (d'Orbigny) from Pictet, 1859, pl. 17, fig. 1b, diameter 95 mm.

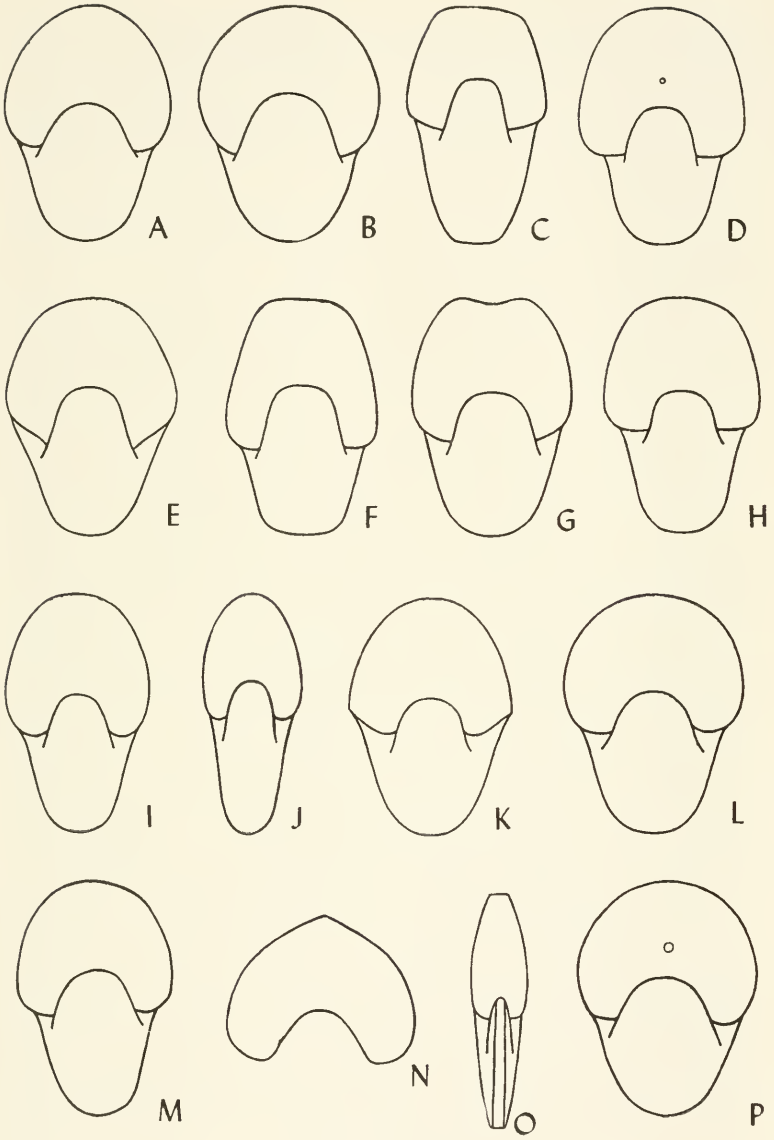

Figure 23

(Department de l'Aube), where the species was found.

"But the drawing given by d'Orbigny is faulty; first its dimensions do not agree with the description; then the drawing being reduced to one-third the natural size, the specimen which it represents should have been at least 360 mm. in diameter; besides, the ornaments are wanting in the drawing on a great part of the last whorl. . . .

"Consider then the figure by d'Orbigny as only approximate. D'Orbigny has restored a great many of his plates, for which, in my opinion, he is very much to blame. . . .

"In the d'Orbigny collection no specimen is specially marked as the type. But d'Archiac (Hist. du progrès de la géologie, vol. iv, p. 295) quotes *N. pseudoelegans*, and he has given to the Museum a specimen marked *type*. This specimen is small (greatest diameter 150 mm.), and agrees neither with the figure nor with the dimensions given in d'Orbigny's original description.

"Perhaps the true type was contained in the collection of the geologist Clément Mullet, who showed d'Orbigny over the locality where *N. pseudoelegans* abounds?" In accordance with the above statement Foord and Crick (1890a, p. 551) in the legend of their figure 3, state that the drawing is from a specimen in the d'Orbigny Collection in the Museum of Natural History, Paris. However, Foord (1891, p. 255, fig. 59 a, b) labelled the same figure as drawn from d'Orbigny's type specimen.

The type specimen is a much inflated conch, very involute and with a small umbilicus. The whorl section is wider than high with a broadly rounded venter. Whorl sides are also broadly rounded. The test bears prominent ribs that are sigmoidal on the whorl sides and form a sinus on the venter. The suture is only slightly sinuous with shallow ventral and lateral lobes. The siphuncle lies below the center of the septa.

There are approximately 64 species of *Cymatoceras* recorded to date. All of these are characterized by the ribbing and the slightly sinuous septa. The shape of the whorl section is quite variable in this genus (Fig. 23). The type species, *C. pseudoelegans,* has a depressed, globular conch; one of the most compressed conchs is that of *C. neocomiensis* (d'Orbigny) (Fig. 23 *J*). Between these two extremes there are all gradations of

conch patterns with well rounded venters. Whereas most of the species are very involute, as in the type, there is a wide range of variation to rather evolute species as *C. patens* (Kner, 1850) and *C. tskaltsithelensis* (Rouchadzé, 1931). Some of the species develop sharply rounded to subangular shoulders. *Cymatoceras tourtiae* (Schlüter) has a subquadrate whorl section with subangular ventral and umbilical shoulders; the venter is low and arched (Fig. 23*C*). The juvenile volutions, however, have broadly arched venter with well rounded ventral shoulders (Schlüter, 1876, pl. 46, fig. 4). *Cymatoceras deslongchampsianum* (d'Orbigny) has an arched venter with rounded ventral shoulders but subangular umbilical shoulders with a sloping, slightly arched umbilical wall (Fig. 23*K*). *Nautilus vaelsensis* Binckhorst (1861, p. 15, and Schlüter 1876, p. 57) is one of the most aberrant cymatoceratids known to me and is made the type of a new genus (p. 439). The conch is very compressed and evolute. The whorl sides are slightly convex with broadly rounded umbilical shoulders and angular ventral shoulders; the venter is flattened. The test bears the typical cymatoceratid ribbing. The characters of the ventral area, that is, the flattened venter and the angular ventral shoulders, are also found in *Heminautilus*. This latter genus, however, is very involute and the whorl sides are generally slightly inflated near the umbilical shoulders. *Cymatoceras tourtiae* also has the flattened venter and angular shoulders, but the conch is inflated, involute and the whorl section subquadrate.

The position of the siphuncle in the type species (*C. pseudoelegans*) is below the center — that is, closer to the dorsum than the venter (d'Orbigny, 1840, pls. 8, 9; Foord, 1891, p. 256). It appears that this condition prevails in a majority of the species of *Cymatoceras* (e.g. *C. neocomiensis, C. radiatus, C. gabbi, C. colombiana, C. elegans, C. kayeanus, C. kossmati,* and *C. cenomanensis*). The siphuncle lies above the center, that is closer to the venter than the dorsum in *C. atlas, C. tenuicostatus,* and *C. hunstantonensis*. A specimen of *C. loricatus* (Schlüter) figured by Griepenkerl (1889) has a near marginal (ventral) siphuncle.

The suture of *C. pseudoelegans* is only slightly sinuous with shallow ventral and lateral lobes. *Paracymatoceras* differs from *Cymatoceras* essentially only in the greater sinuosity of its suture (Fig. 24). As noted by Miller and Harris (1945, p. 10) these two genera are more or less gradational in respect to the

suture. Those specimens with more sinuous sutures, and thus transitional to *Paracymatoceras*, include *C. colombiana* (Fig.

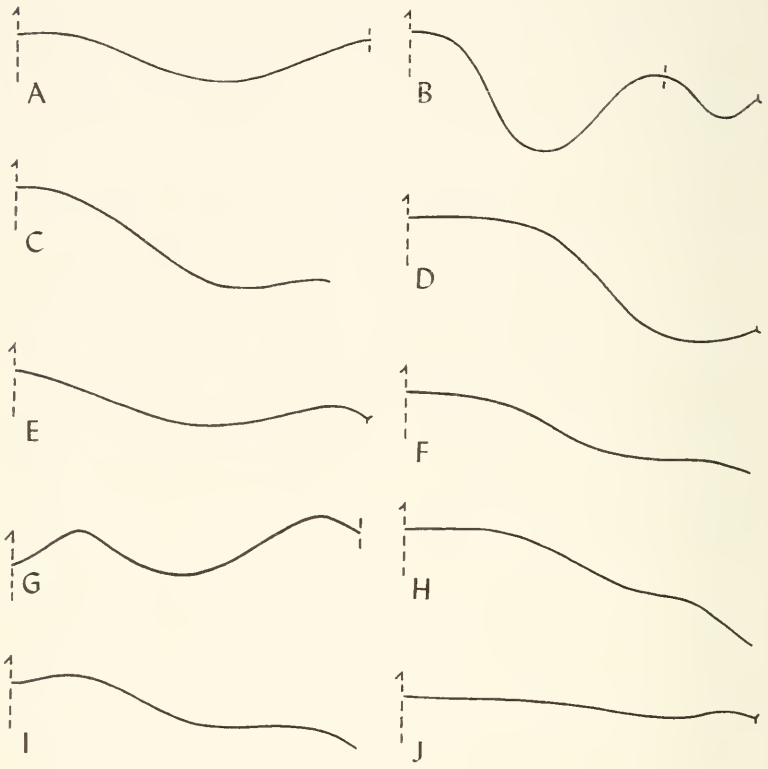

Fig. 24. Diagrammatic representation of sutures of *A*, *Cymatoceras colombiana* Durham 1946, fig. 3G; *B*, *Paracymatoceras texanum* (Shumard) 1860, from Miller and Harris 1945, fig. 3A; *C*, *Cymatoceras pseudonegama* (Spengler) 1910, pl. 12, fig. 7d; *D*, *C. semilobatus* (Spengler) 1910, pl. 11, fig. 4b; *E*, *C. hilli* (Shattuck) from Miller and Harris 1945, fig. 2A; *F*, *C. kayeanum* (Blanford), from Spengler, 1910, pl. 12, fig. 7*2*; *G*, *C. tskaltsithelensis* (Rouchadzé) 1931, fig. 6; *H*, *C. kossmati* (Spengler) 1910, fig. 7b; *I*, *C. virgatum* (Spengler) 1910, fig. 7c; *J*, *C. lochlichi* Miller and Harris 1945, fig. 2C. All figures greatly reduced.

24A), *C. cenomanensis*, *C. tourtiae*, *C. patens*, *C. semilobatus* (Fig. 24 *D*), *C. kossmati* (Fig. 24 *H*), and *C. virgatum* (Fig. 24 *I*). The type species does not have an annular lobe, which appears to be the case in the majority of species of *Cymatoceras*. However annular lobes in the center of the dorsal lobe are present in *C. radiatus*, *C. loeblichi*, *C. colombiana*, and *C. tourtiae*. Most species of *Cymatoceras* have broad ventral saddles but some as *C. virgatum* (Spengler) and *C. tskaltsithelensis* (Rouchadzé) have very pronounced ventral lobes.

Cymatoceras is the most common, and has a larger number of species than any of the other genera of the Cymatoceratinae. All members of this subfamily have in common the characteristic ribbing. The other genera are differentiated on the basis of specialization of the ribbing, shape of conch, or suture. *Procymatoceras* has a depressed, rapidly expanding conch, with whorl sides and venter flattened. *Eucymatoceras* has the inflated rounded conch as in *Cymatoceras pseudoelegans* but the ribs form V-shaped patterns on the venter and on the whorl sides. *Paracymatoceras* is like *Cymatoceras* except for the greater sinuosity of the suture which has a well developed lateral lobe and a saddle at the umbilical suture. *Cymatonautilus* has a depressed evolute conch with concave lateral and ventral areas. *Syrionautilus* has acute, widely spaced, and nearly straight ribs. *Anglonautilus* has a depressed whorl section with large transverse undulations on the venter. *Heminautilus* has a much compressed conch, with a flattened venter, and a very sinuous suture. *Epicymatoceras* has a compressed, evolute conch with subquadrate whorl section. *Deltocymatoceras* has a subtriangular whorl section.

As stated above in the discussion of the subfamily Cymatoceratinae, *Neocymatoceras* Kobayashi (1954a) is thought to fall within the range of variation of *Cymatoceras* and is placed in synonymy of that genus.

Cymatoceras is characteristic of the Cretaceous. Steuer (1921) has described *Cymatoceras perstriatus* (Steuer) from very late Jurassic and earliest Cretaceous strata of Argentina. *Cymatoceras tsukushiense* (Kobayashi, 1954a) comes from Oligocene strata of Japan. These two are the only non-Cretaceous species of *Cymatoceras* known to the writer. *Cymatoceras* is worldwide in distribution (Figs. 21, 22).

DISTRIBUTION OF SPECIES OF THE GENUS CYMATOCERAS

Species	Stratigraphic Distribution	Geographic Distribution
C. albensis (d'Orbigny) 1850	Cretaceous	England, France
C. altavensis (Pomel) 1889	Cretaceous (Neocomian)	Algeria
C. andranofotsyense Collignon, 1951	Cretaceous (Albian)	Madagascar
C. anguliferous (Schlüter) 1876	Cretaceous (Cenomanian)	Germany
C. articulatus (Pulteney) 1813	Cretaceous	England
C. atlas (Whiteaves) 1876	Cretaceous (Upper)	England, France
C.? averilli (Anderson) 1938	Cretaceous (Lower)	California (U.S.A.)
C. bayfieldi (Foord and Crick) 1890	Cretaceous (Senonian)	England
C. bifurcatum (Ooster) 1858	Cretaceous	Switzerland
C. broitzemensis (Müller and Wollemann) 1906	Cretaceous (Senonian)	Germany
C.? campbelli (Meek) 1861	Cretaceous	Vancouver Island, B.C.
C. carlottensis (Whiteaves) 1900	Cretaceous (Upper)	Maple Island, B.C.
C. cenomanensis (Schlüter) 1876	Cretaceous (Cenomanian)	Europe
C. colombiana Durham, 1946	Cretaceous (Aptian)	Colombia
C. compressus (Tavani) 1942	Cretaceous (Albian)	Somaliland
C. crebricostatus (Blanford) 1861	Cretaceous (Albian)	India
C. deslongchampsianum (d'Orbigny) 1840	Cretaceous (Neocomian-Cenomanian)	Europe
C. eichwaldi (Karakasch) 1907	Cretaceous (Lower)	Crimea
C. elegans (J. Sowerby) 1816	Cretaceous (Cenomanian)	England
C. elegantoides (d'Orbigny) 1840	Cretaceous (Cenomanian)	England, France

Species	Stratigraphic Distribution	Geographic Distribution
C. formosus (Blanford) 1861	Cretaceous (Senonian)	India, Madagascar
G. gabbi (Anderson) 1902	Cretaceous (Lower)	California (U.S.A.)
C. guilielmi telli (Ooster) 1858	Cretaceous	Switzerland
C. hilli (Shattuck) 1903	Cretaceous (Lower)	Texas (U.S.A.)
C. hunstantonensis (Foord and Crick) 1890	Cretaceous (Cenomanian)	England
C. huxleyanus (Blanford) 1861	Cretaceous (Turonian)	South India, Madagascar
C. imbricatus (Crick) 1907	Cretaceous	Natal, Africa
C. interstriatus (Strombeck) 1863	Cretaceous (Upper)	Germany
C. kayeanus (Blanford) 1861	Cretaceous (Albian-Cenomanian-Turonian)	India, Madagascar
C. kossmati (Spengler) 1910	Cretaceous (Albian)	India
C. loeblichi (Miller and Harris) 1945	Cretaceous (Lower)	Texas (U.S.A.)
C. loricatus (Schlüter) 1876	Cretaceous (Senonian)	Germany
C. madagascarensis (Yabe and Shimizu) 1924	Cretaceous (Upper)	Madagascar
C. manuanensis (Crick) 1907	Cretaceous (Albian)	Natal, Africa
C. mikado (Krenkel) 1910	Cretaceous (Neocomian)	Tanganyika
C. nebrascense (Meek and Hayden) 1862	Cretaceous (Upper)	Montana (U.S.A.)
C. neckerianus (Pictet) 1847	Cretaceous (Aptian, Albian)	Europe
C. negama (Blanford) 1861	Cretaceous (Albian)	India
C. neocomiensis (d'Orbigny) 1840	Cretaceous (Lower)	Europe, Crimea
C. neohispanicum (Burckhardt) 1925	Cretaceous (Aptian)	Mexico

Species	Stratigraphic Distribution	Geographic Distribution
C. occlusus Crick, 1907	Cretaceous	Zululand
C. patens (Kner) 1850	Cretaceous (Senonian)	Poland, Germany
C. perstriatus (Steuer) 1921	Jurassic (Upper) Cretaceous (Lower)	Argentina
C. pseudoatlas (Yabe and Shimizu) 1924	Cretaceous (Upper)	Japan
C. pseudoelegans (d'Orbigny) 1840	Cretaceous	Europe
C. pseudonegama Spengler, 1910	Cretaceous (Albian)	India
C. pseudonokomiense Shimizu, 1931	Cretaceous (Aptian)	Japan
C. radiatus (J. Sowerby) 1822	Cretaceous	Europe
C. sakalavum Collignon, 1949	Cretaceous (Albian)	Madagascar
C. saussureanus (Pictet) 1847	Cretaceous (Albian)	Switzerland
C. scecqurensis (Tavani) 1942	Cretaceous (Albian)	Somaliland
C. semilobatus Spengler, 1910	Cretaceous (Albian)	India
C. semiundatus (Foord) 1891	Cretaceous (Cenomanian)	England
C. sharpei (Schlüter) 1876	Cretaceous (Cenomanian)	Germany
C.? sinuatoplicatus (Geinitz) 1843	Cretaceous (Upper)	Germany
C. straticostatus (Crick) 1907	Cretaceous	Natal, Africa
C. suciense (Whiteaves) 1879	Cretaceous (Upper)	Sucia Island Group, B. C.
C. tenuicostatus (Schlüter) 1876	Cretaceous (Cenomanian)	Germany
C. tourtiae (Schlüter) 1876	Cretaceous (Cenomanian)	Germany
C. tskaltsithelensis (Rouchadzé) 1931	Cretaceous (Aptian)	Russia
C. tsukushiense (Kobayashi) 1954	Oligocene	Japan
C. undulatiformis Spath, 1927	Cretaceous (Neocomian)	Tanganyika

Species	Stratigraphic Distribution	Geographic Distribution
C. ventroplicatus (Foord) 1891	Cretaceous (Cenomanian)	England
C. virgatus (Spengler) 1910	Cretaceous (Albian)	India
C. woodsi (v. Hoepen) 1921	Cretaceous (Upper)	South Africa

Genus PARACYMATOCERAS Spath, 1927

Paracymatoceras Spath, 1927a, pp. 21, 25.

Paracymatoceras Miller and Harris, 1945, p. 9.

Paracymatoceras Kummel, 1953a, p. 4.

Type species. Nautilus asper (Oppel) Zittel, 1868, pl. 3, fig. 1 (by original designation). Illustrated on Plate 19, figures 1, 2 and Text Figure 23*G*, of this report.

Most of the other genera of the Cymatoceratinae are distinguished from *Cymatoceras* on differentiations of the conch form or sculpture. *Paracymatoceras* differs from *Cymatoceras* essentially only in the greater elaboration of the suture. It is also generally agreed that in respect to the suture *Cymatoceras* and *Paracymatoceras* intergrade (Fig. 24). The conch form, degree of involution, and shell sculpture agree perfectly with *Cymatoceras*. The type species — *P. asper* — which is of Upper Jurassic age, has a rounded ventral groove on the most adoral part of the living chamber (Fig. 23*G*). This feature is not present in any of the five Cretaceous species of *Paracymatoceras* known to date. Aside from the ventral groove in the type species, the conch form in the other species assignable to *Paracymatoceras* are completely similar to or within the range of variation of *Cymatoceras*.

Six species can be assigned to this genus ranging in age from Upper Jurassic through the Cretaceous. Four of the species are Lower Cretaceous in age. The genus does not appear to be a common element in nautiloid faunas but it has been recorded from India, Europe, Texas, and Mexico (Figs. 21, 22). Some juvenile forms from the Lower Cretaceous Pawpaw formation of Texas with perfectly smooth conchs have been recorded by Kummel (1953a). These specimens are of interest in emphasizing the difficulties in identifying weakly-ribbed *Paracymatoceras* and differentiating these from *Hercoglossa*.

DISTRIBUTION OF SPECIES OF THE GENUS PARACYMATOCERAS

Species	Stratigraphic Distribution	Geographic Distribution
P. asper (Oppel) 1865	Jurassic (Upper)	Europe
P. karpinskyi (Karakasch) 1907	Cretaceous (Lower)	Crimea
P.? milleri Humphrey, 1949	Cretaceous (Aptian)	Durango, Mexico
P. rota (Blanford) 1861	Cretaceous (Albian, Maestrichtian)	South India, Madagascar
P. texanum (Shumard) 1860	Cretaceous (Lower)	Texas (U.S.A.)
P. trichinopolitensis (Blanford) 1861	Cretaceous (Senonian)	South India; East Indies?

Genus PROCYMATOCERAS Spath, 1927

Procymatoceras Spath, 1927a, pp. 21, 25.

Procymatoceras Miller and Harris, 1945, p. 11.

Type species. Nautilus subtruncatus Morris and Lycett, 1850, pl. 1, fig. 2 (by original designation).

The genotype described and figured by Morris and Lycett does not seem to be available. Several topotype specimens are in the collections of the British Museum (Natural History) one of which is illustrated on Plate 17 and the cross section of the same specimen in Text Figure 25. From a study of topotype specimens and the original description of the type species the following diagnosis of *Procymatoceras* can be made.

The conch is robust, rapidly expanding, very involute to occluded. Whorl section generally wider than high. On the living chamber the venter and whorl sides are flattened. The ventral and umbilical shoulders are well rounded. The whorl sides converge towards the venter. The earlier volutions are more rounded in outline. The surface of the conch bears sinuous ribs that form a broad sinus on the venter. The ribs appear to be fasciculate growth lines and may not be homologous with those of typical *Cymatoceras*. The ribbing is most distinct on the living chamber. The sutures are only slightly sinuous with shallow ventral and dorsal lobes.

When Spath (1927a) first established *Procymatoceras* he included only the type species and *P. baberi* (Morris and Lycett) both from the Middle Jurassic of Great Britain. The topotype specimen of *P. subtruncatus* illustrated on Plate 17, and on Text

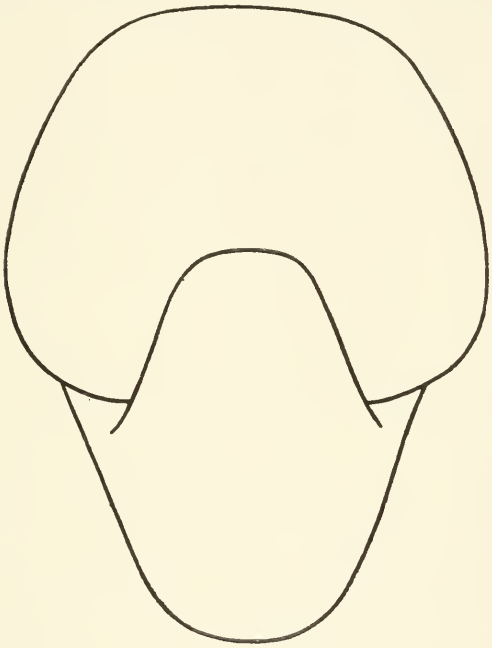

Fig. 25. *Procymatoceras subtruncatus* (Morris and Lycett). Diagrammatic cross section of topotype represented by figures 1, 2, Plate 17, X 0.50.

Figure 25, clearly shows the robust involute character of the conch and the subtrapezoidal outline of the whorl section. Neither the suture nor the siphuncle are visible. *Nautilus intumescens* Waagen has been referred with question to *Procymatoceras*. I agree with Spath (1927a, p. 33) that it is doubtful whether Noetling's (1896) specimens from Baluchistan assigned to *N. intumescens* Waagen are correctly identified. The only

other species that appears to belong to this genus is *Paracenoceras costatum* Scott (1943).

Genus CYMATONAUTILUS Spath, 1927

Cymatonautilus Spath, 1927a, p. 21.
Cymatonautilus Miller and Harris, 1945, p. 9.
Type species. Nautilus julii (Baugier MS) d'Orbigny, 1850, p. 328 (by original designation).

The type species of this unusual Jurassic cymatoceratid was originally briefly diagnosed but not illustrated by d'Orbigny (1850, p. 328) who gave Baugier the credit as author of this species. However, Baugier's name apparently was only a manuscript name, and was never published by him. The first complete description and illustration of *Nautilus julii* was published by Guéranger (1865, p. 189, pl. 3). Guéranger's figures are reproduced here on Plate 18, figures 1-4.

This genus can be diagnosed as follows: Conch widely umbilicate, robust, whorls subquadratic, being slightly wider than high. The whorl sides are flattened and with a broad lateral groove. The venter is likewise flattened and with a median groove. The conch bears sinuous ribs that obliquely cross the suture and form a deep ventral sinus. The suture forms a shallow ventral lobe and a broad concave lateral lobe. The siphuncle is subcentral in position, being closer to the dorsum than the venter. The type specimen came from strata of Callovian age in France. Petitclerc (1926) has described and illustrated a specimen of the same species from strata of Bathonian age in France. *Nautilus mojsisovicsi* Neumayr (1870) from Upper Jurassic strata of Austria most probably also belongs in *Cymatonautilus*.

The most distinctive features of this genus are the wide umbilicus and the grooved venter and whorl sides. Most species of the Cymatoceratinae are involute forms.

Genus ANGLONAUTILUS Spath, 1927

Anglonautilus Spath, 1927a, pp. 21, 25.
Anglonautilus Miller and Harris, 1945, p. 8.
Type species. Nautilus undulatus J. Sowerby, 1813, pl. 40, upper figure (by original designation).

Sowerby's type specimen does not appear to be in the British Museum, but the specimen referred to by Foord (1891, p. 245) labelled "*Nautilus undulatus*, M. C. 182" in Sowerby's handwriting is figured here, Plate 20, figures 1, 2, and Text Figure 26. This specimen is also numbered B.M.N.H. 66336. Dr. L. F. Spath kindly informs me that this specimen is unlocalized, but

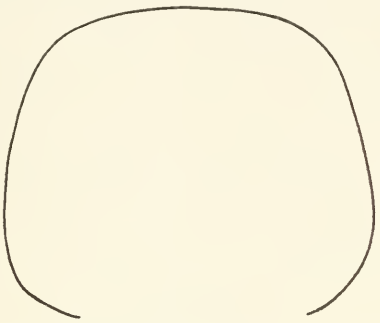

Fig. 26. *Anglonautilus undulatus* (Sowerby). Diagrammatic cross section of adoral part of living chamber of topotype represented by figures 1, 2, Plate 20, X 1.

undoubtedly is a topotype from Nutfield, Surrey. This specimen is incomplete consisting only of two camerae of phragmocone and one-third whorl of living chamber. However, it shows clearly the most diagnostic feature of the genus, that is the large, fold-like undulations which are most prominent on the venter and decrease rapidly on the flanks. The suture forms a very shallow ventral lobe and a broad shallow lateral lobe. The siphuncle is subcentral in position being nearer the dorsum than the venter.

In addition to the type species which is known from Aptian to Cenomanian strata in England and various localities in Europe (*fide* Foord, 1891, p. 244), *Nautilus subalbensis* Sinzow (1913) and *N. begudensis* Kilian and Reboul (1915) should be included in *Anglonautilus*. The former species is from Albian strata in the Crimea and the latter from Hauterivian strata in southern France.

Genus Eucymatoceras Spath, 1927

Eucymatoceras Spath, 1927a, pp. 21, 22, 25.

Eucymatoceras Miller and Harris, 1945, p. 9.

Type species. Nautilus plicatus Fitton, 1835, p. 129 (by original designation).

The type specimen was not available for study but several conspecific forms are in the British Museum. One of these specimens from the Lower Greensand, Atherfield, Isle of Wight (B.M.N.H. C335) is illustrated on Plate 21, and the cross section

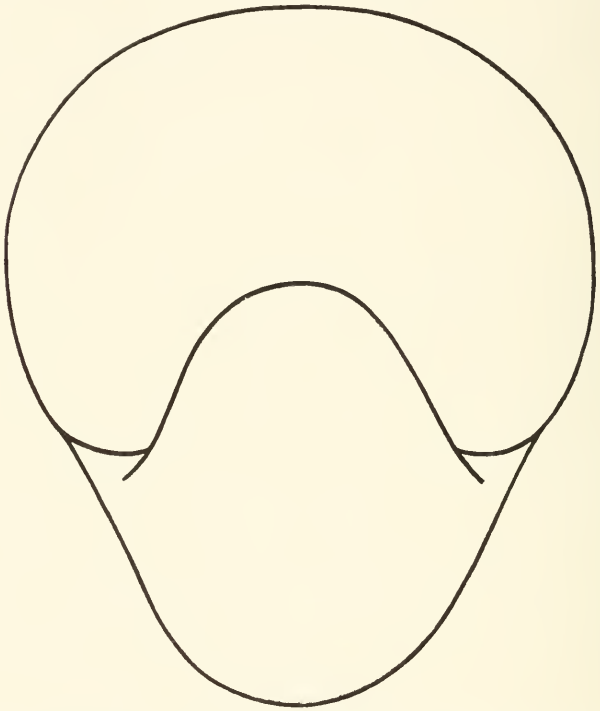

Fig. 27. *Eucymatoceras plicatus* (Fitton). Diagrammatic cross section of plesiotype represented by figures 1, 2, Plate 21, X 1.

in Text Figure 27. The only previous illustrations of the type specimen are the original woodcut in Fitton (1835, p. 129) and figures in d'Orbigny (1840, pl. 10; *Nautilus requienianus* d'Orbigny 1840 =*N. plicatus* Fitton 1835) and in Uhlig (1883, pl. 3).

The genus can be diagnosed as follows: Conch subglobular, involute, umbilicus closed, whorl section rounded, broader than high. Suture only slightly sinuous. The siphuncle is small and subcentral. Surface of conch with prominent ribs that form a deep angular V-shaped ventral sinus and on the whorl sides a similar but asymmetrical salient.

The most diagnostic feature is the V-shaped pattern of the ribs by which it can easily be distinguished from any other genus of the Cymatoceratinae. At present only three species of *Eucymatoceras* have been recorded, namely *N. plicatus* Fitton, the type species, and *N. steveni* Karakasch (1907, p. 30, pl. 2, fig. 13; pl. 8, fig. 12) from Lower Cretaceous formations of the Crimea; and *N. stschurouskii* Milaschevitch, (1877, p. 125, pl. 1, figs. 11, 11a) from the Lower Cretaceous of Russia. All of these species have the depressed, subglobular, rounded conchs. From the great variability in conch form in *Cymatoceras* it is doubtful if the conch form in the known species of *Eucymatoceras* can be considered a diagnostic character.

Genus SYRIONAUTILUS Spath, 1927

Syrionautilus Spath, 1927a, pp. 21, 25.
Syrionautilus Miller and Harris, 1945, p. 11.
Syrionautilus Avnimelech, 1946, pp. 523-528; 1947a, p. 690.
Type species. Nautilus libanoticus Foord and Crick, 1890, p. 404, fig. 6 (by original designation).

All the specimens of *Nautilus libanoticus* in the British Museum (Natural History) upon which Spath established his genus *Syrionautilus* are more or less crushed and distorted. One of the syntypes with an attached mandible is figured here on Plate 7, figure 3 (previously figured by Foord, 1891, p. 371, fig. 82.). The general form of the conch is like that of *Cymatoceras* but the character of the ribbing is quite distinct. In *Syrionautilus* the ribs are acute and separated by interspaces rather exceeding their own width. The type of ribbing is very similar to that of *Proclydonautilus spirolobus* of the Upper Triassic. The form and spacing of the ribs in *Syrionautilus* are the distinguishing characters that serve to separate it from allied genera of the Cymatoceratinae. The position of the siphuncle and nature of the suture are not known. The type and only

species so far referable to this genus comes from Senonian formation of Syria.

Recently Avnimelech (1946, 1947a) has published two short notes on additional specimens of *Syrionautilus libanoticus* from Palestine. As with the types, this new material is also incomplete and generally crushed. However, the best and nearly complete specimen was figured by Avnimelech (1947a, pl. 15). Even though this figured specimen is also compressed it clearly shows *Syrionautilus* to have an involute, compressed conch and arched venter. In other words, it has a typical cymatoceratid conch but differs in the character of the ribs.

Genus HEMINAUTILUS Spath, 1927

Heminautilus Spath, 1927a, pp. 22, 25.
Vorticoceras Scott, 1940, pp. 1074, 1075.
Heminautilus Scott 1943, p. 89.
Heminautilus Durham, 1946, p. 432.
Platynautilus Yabe and Ozaki, 1953, pp. 55-61.
Type species. Nautilus saxbii Morris, 1848, p. 106 (woodcut); Pl. 10, figs. 1, 2 of this report (by original designation).

When Spath established this genus he designated *Nautilus saxbii* Morris (1848, p. 106, woodcut) as genotype and thought this species was the same as *N. lallierianus* d'Orbigny (1841). The latter species was first very briefly diagnosed but not illustrated by d'Orbigny in 1941 in the Revue Cuvierienne (p. 318), and was listed the same year in his Paléontologie Francaise. Terrains Crétacés (p. 620). *Nautilus lallierianus* was again cited by d'Orbigny in his Prodrome (1850, t. 2, p. 112), and *N. saxbii* was listed as a synonym. In none of these publications is there an illustration and only the first (1841, p. 318) has a very brief diagnosis. *N. lallierianus* was next described and illustrated from Switzerland by Pictet and Campiche (1859). Douvillé (1916) gave a very complete description with several figures of specimens of *N. lallierianus* from Aptian strata east of Suez. Douvillé likewise placed *N. saxbii* in synonymy of *N. lallierianus*. Foord (1891) recognized both of these species.

The type specimen of *Nautilus saxbii* is illustrated on Plate 10, figures 1, 2, and the cross section in Text Figure 28. The only previous illustrations of this specimen are the woodcuts in Morris (1848, p. 106) and Foord (1891, p. 311, fig. 68). Since

d'Orbigny's *N. lallierianus* has not been illustrated, and the description is very brief, it is impossible to tell whether it is conspecific with *N. saxbii*. *Nautilus lallierianus*, Douvillé (1916) is sufficiently distinct from *N. saxbii* Morris in the form of the septa and ornamentation of the conch to keep these two species separate. The plaster casts of the specimen of *N. lallierianus* figured by Pictet and Campiche (1859, pl. 19, figs. 6a, 6c) are in the Museum of Comparative Zoology. These show no surface ornamentation whatsoever. The tricarinate character of the venter is not as well preserved as the figures by Pictet and Campiche would lead one to believe.

The genus *Heminautilus* can be diagnosed as follows: Conch involute, very compressed, whorls much higher than wide. Whorl sides flattened and strongly converge towards a narrow, flattened or slightly concave venter. The ventral shoulders are angular. The venter on the earlier volutions is rounded. The umbilical shoulders are broadly rounded. Greatest width of the conch is just ventral of the umbilical shoulders. The suture is rather sinuous with a ventral lobe, a subangular saddle on the ventral shoulder, broad deep lateral lobe and a narrowly rounded saddle on the umbilical shoulder. The siphuncle is subcentral in position lying closer to the dorsum than the venter. The conch bears sinuous ribs that curve strongly aborally over the ventral half of the whorl side. The ribbing may be very weak and in fact is absent on the type of *Nautilus saxbii* (which is probably a juvenile).

Spath originally placed *Heminautilus* in his Paracenoceratidae with question and made note of the possibility that it more properly belonged in his Cymatoceratidae. The Paracenoceratinae are characterized by differentiation of the periphery, generally associated with increase in sinuosity of the suture line, and a ventral lobe (Spath, 1927a, p. 25). However, the sutures of *Heminautilus* are much more sinuous (Fig. 20). The Paracenoceratinae have smooth shells, devoid of ribbing. *Tithonoceras*, and *Aulaconautilus* have longitudinal ribs or carinae on the ventral area but no sculpture on the flanks. Sinuous cymatoceratid-like ribbing is characteristic of *Heminautilus*. The ribbing is well preserved on the specimens of *H. lallierianus* figured by Douvillé (1916, pl. 17, figures 2-6) and on *H. rangei* Hoppe (1922, pl. 4, figures 2, 3). Among the specimens illus-

trated by Douvillé there is some variability in the strength and patterns of the ribs. On the earlier volutions the ribs are low, broad, and rounded and decrease towards the venter. The mature specimen of Douvillé's (1916) figure 5, plate 17, has a smooth outer volution, whereas the larger specimen of figure 6a, b, shows prominent ribs that are very broad and separated by narrow concave interspaces. In *Heminautilus etheringtoni* Durham (1946) the ribs are most prominent on the living chamber

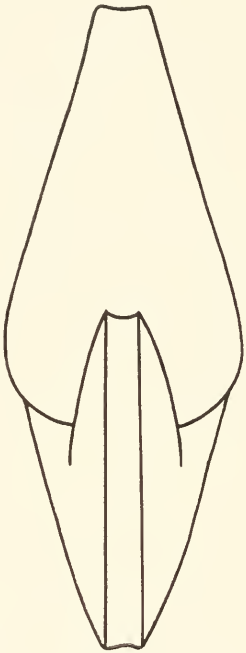

Fig. 28. *Heminautilus saxbii* (Morris). Diagrammatic cross section of holotype represented by figures 1, 2, Plate 10, X 1.

which is about one-third of a volution in length. Topotype specimens of *Heminautilus etheringtoni* kindly loaned to me by J. Wyatt Durham show rather distinct ribbing on early volutions. with a single large topotype smooth except for prominent growth

lines. A crushed and weathered specimen, not referred to by Durham (1946), from near the top of the basal Velez Sandstone measures approximately 145 mm. in diameter and has very prominent "cymatoceratid" ribs. The ventral area likewise appears to have a median longitudinal rib. With the material available it cannot be determined whether or not this specimen is conspecific with *H. etheringtoni*. They do not come from the same horizon within the Aptian. No data are available on the degree and extent of variation in the sculpture of this or most species of nautiloids. It is very rare that really representative populations can be collected.

Heminautilus tyôsiensis (Yabe and Ozaki) 1953, shows prominent growth lines on the venter that form a deep V-shaped pattern. On the lateral whorl sides low radial folds with broader intervals are present on the type (and only) specimen of this species. These authors proposed a new genus — *Platynautilus* — for their new species, but it is clearly a representative of *Heminautilus* and thus *Platynautilus* is placed in synonymy.

Heminautilus stantoni (Scott) has broad, low, rounded and widely spaced ribs reaching their greatest prominence on the middle of the flanks. *Heminautilus saxbii,* the type specimen which is figured here on Plate 10, figures 1, 2, is perfectly smooth but is probably not a mature specimen.

The suture in most species of the Cymatoceratinae are only very slightly sinuous. *Paracymatoceras* has a well-developed, deep, lateral lobe followed by a saddle on the umbilical shoulder. The suture across the venter generally develops a ventral saddle, not a lobe. *Cymatonautilus julii* has a deep ventral lobe, and a broad lateral lobe with the beginnings of a saddle on the umbilical region. "*Nautilus*" *vaelsensis* (Binckhorst, 1861) is a very compressed form with a subrectangular whorl section and a wide, shallow umbilicus. The truncate venter and compressed conch are very reminiscent of *Heminautilus* except in the difference of involution. The suture of "*Nautilus*" *vaelsensis* has a very shallow ventral lobe and a broad, shallow, lateral lobe.

The six known species of *Heminautilus* are from Lower Cretaceous formations in Arkansas, England, France, Switzerland, Egypt, Palestine, Colombia, and Japan.

DISTRIBUTION OF SPECIES OF THE GENUS HEMINAUTILUS

Species	Stratigraphic Distribution	Geographic Distribution
H. etheringtoni Durham, 1946	Cretaceous (Aptian)	Colombia
H. lallierianus (d'Orbigny) 1840	Cretaceous (Neocomian)	Europe, Egypt, Ethiopia
H. rangei (Hoppe) 1922	Cretaceous (Albian)	Palestine
H. saxbii (Morris) 1848	Cretaceous (Aptian)	England, France
H. stantoni (Scott) 1940	Cretaceous (Aptian)	Arkansas (U.S.A.)
H. tyôsiensis (Yabe and Ozaki) 1953	Cretaceous (Aptian?)	Japan

Genus DELTOCYMATOCERAS n. gen.

Type species. Nautilus leiotropis Schlüter, 1876, p. 175, pl. 48, figs. 1, 2 (Plate 22, figures 1, 2 of this paper).

The adaptive radiation within the Cymatoceratinae is expressed in patterns that are homeomorphous with evolutionary trends in other phyletic lines within the Nautilidae. Modification of rib patterns, conch shape, and suture are the more obvious characters which express evolution within the subfamily. The present genus is established for those cymatoceratids with a more or less triangular outline of the whorl section. The type species — *Nautilus leiotropis*, and *N. rugatus* (Fritsch and Schlönbach) are the only species known to date that can be placed in this genus. The triangular outline of the whorl section serves readily to differentiate this genus from all others within the Cymatoceratinae.

The type species has a large, inflated, involute conch with broadly arched and strongly convergent whorl sides. The venter is marked by a slight rounded, smooth, keel-like ridge. There are no distinct ventral shoulders, the ventral region grading evenly onto the flanks. The flanks have prominent cymatoceratid ribs that bifurcate near the middle of the whorl sides. The ribs do not cross the keel-like ridge on the venter. The suture forms a narrow, somewhat pointed, ventral saddle, a broad,

rather shallow lateral lobe, and a prominent saddle on the umbilical shoulder. The position of the siphuncle is not known.

The distinctive subtriangular whorl section with the smooth keel-like ridge on the venter set *Deltocymatoceras leiotropis* apart from all other cymatoceratids. In conch form and suture pattern *Deltocymatoceras* is homeomorphous with *Angulithes* of the Hercoglossinae, being distinguished by its ribbing. *Angulithes* is most probably a development of *Cimomia*, a form with a more rounded whorl shape. *Deltocymatoceras* is best visualized as a sagittate derivative of *Cymatoceras* which shows much variation in conch shape.

The type species of *Deltocymatoceras* comes from Upper Cretaceous (Emscher-Mergel) of Germany. The original is in the Museum of the University of Bonn (*fide* Schlüter, 1876, p. 175). *Deltocymatoceras rugatus* comes from Upper Cretaceous strata of Bohemia.

Genus EPICYMATOCERAS n. gen.

Type species. *Nautilus vaelsensis* Binckhorst, 1861, p. 15, pl. 5c, figs. 2a, b, c.

This new genus is established for a species of Upper Cretaceous nautiloid that has a most unusual conch shape for post-Triassic nautiloids. The species has been described and figured by Binckhorst (1861, p. 15, pl. 5c, figs. 2a, b, c) and Schlüter (1876, p. 177, pl. 51, figs. 3-4). Schlüter's figure is reproduced here on Plate 23, figs. 1, 2.

Nautilus vaelsensis has an evolute and greatly compressed conch. The umbilical diameter is approximately 25 per cent of the diameter of the conch. The whorl section is subquadrate, being nearly twice as high as wide. The ventral shoulders are angular, the venter narrow and flattened. The lateral flanks are only slightly inflated. The umbilical shoulders are broadly arched. The suture inscribes a very shallow ventral lobe and a shallow lateral lobe. The position of the siphuncle is not known. The conch bears fine sinuous ribs that curve backwards toward the ventral shoulder and form a slight sinus on the venter.

Epicymatoceras is distinguished from all other genera of the Cymatoceratinae by its compressed, evolute conch and flattened venter. It is the ribbing which attaches this genus to the Cyma-

toceratinae. Among the Cymatoceratinae the only group somewhat similar is *Heminautilus* which is likewise compressed in conch form and with a flattened venter. However, in *Heminautilus* the whorl section is much more inflated near the umbilical shoulders and the flanks more convergent. Likewise this genus is very involute and with a more sinuous suture. Most of the remaining genera and species of the Cymatoceratinae have more involute and inflated conchs.

The presence of cymatoceratid ribbing readily differentiates *Epicymatoceras* from other subfamilies of the Nautilidae. There is some similarity in conch shape of *Epicymatoceras* with that of *Pseudocenoceras* of the Nautilinae. However, in that genus the smooth conch has a well rounded ventral area ,steep umbilical shoulders, and is more involute.

The type and only species of this genus has been identified from Upper Cretaceous (Maestrichtian) strata at Vaels near Achen (Germany) and at Limbourg (Belgium) just south of Achen.

Subfamily HERCOGLOSSINAE Spath, 1927

Spath (1927a) originally erected this family to include the following genera: *Pseudaganides* Spath of the Jurassic and lowermost Cretaceous; *Hercoglossa* Conrad, Upper Cretaceous to Eocene; *Hercoglossoceras* Spath, Liassic; *Pseudonautilus* Meek, Upper Jurassic; *Paraturia* Spath (=*Aturoidea* Vredenburg), Cretaceous to Eocene; and *Deltoidonautilus* Spath, Eocene. Later he (Spath 1927b) included *Cimomia* Conrad, and Stenzel (1940) added his genus *Woodringia*. Restudy of this group alters the above interpretation in many important details. The Jurassic hercoglossids, namely *Pseudaganides* and *Pseudonautilus* are interpreted as a distinct phyletic line from the Cretaceous-Eocene trend involving *Hercoglossa* itself (see page 389). *Hercoglossoceras* is considered to be a synonym of *Pseudaganides*. It is merely an early, highly compressed "aganitici" and is part of the radiation from the cenoceratid complex which went in for highly modified sutures (Pseudaganitinae). Adaptation towards modified (highly sinuous) sutures is a trend that has occurred many times in the evolutionary history of the nautiloids. Within the Upper Paleozoic few nautiloids are known with

highly sinuous sutures. The most extreme development is that found in *Permoceras bitauniensis* (Haniel) from strata of Leonard age in Timor. *Grypoceras* (*Plummeroceras*) *plummeri* Kummel (1953c) of the Grypoceratidae from beds of Leonard age in Texas has a deep ventral lobe and lateral lobe. When Miller and Collinson (1953) established the genus *Permoceras* they also erected the family Permoceratidae for their monotypic genus. It appears more likely that *Permoceras* is an aberrant development from the *Domatoceras-Grypoceras* evolutionary line and should be included in the Grypoceratidae.

In the Triassic, the first large-scale adaptation towards highly modified sutures appears in the Clydonautilidae, Gonionautilidae, and Siberionautilidae all of the Upper Triassic. The sutural patterns seen in these groups are closely similar to those of the *Pseudaganides-Pseudonautilus* trend of Jurassic age and to the *Hercoglossa-Aturoidea* trend of Cretaceous-Eocene age. The details have been discussed previously (p. 389) and the evidence seems quite strong that in the Mesozoic there were three separate radiations built largely around modification of the suture, the first in the Triassic, the second in the Jurassic, and the third in the Cretaceous. A similar adaptive trend also took place in the Cymatoceratinae. Since the basic sutural type must surely be an adaptive character it is no more than to be expected that repetition of similar forms will be produced. For the above reasons *Pseudaganides* and *Pseudonautilus* are considered a separate phyletic development and placed in the subfamily Pseudaganidinae.

Deltoidonautilus Spath is considered to be a synonym of *Angulithes* Montfort (Kummel 1953a)). Spath placed *Angulithes* in the Nautilidae but it is here considered part of the Hercoglossinae. *Woodringia* Stenzel (1940) is placed as a synonym of *Hercoglossa* since the character upon which it was distinguished — a slight ventral lobe in the ventral saddle — is of no more than specific importance in other genera of this subfamily.

Thus, as now interpreted, the Hercoglossinae include the following genera: *Hercoglossa* Conrad, *Cimomia* Conrad, *Angulithes* Montfort, and *Aturoidea* Vredenburg. These genera are all characterized by involute, smooth, conchs with modified sutures. As has been shown by Miller (1947, 1949) on several occasions this group of genera appears to form a linear series

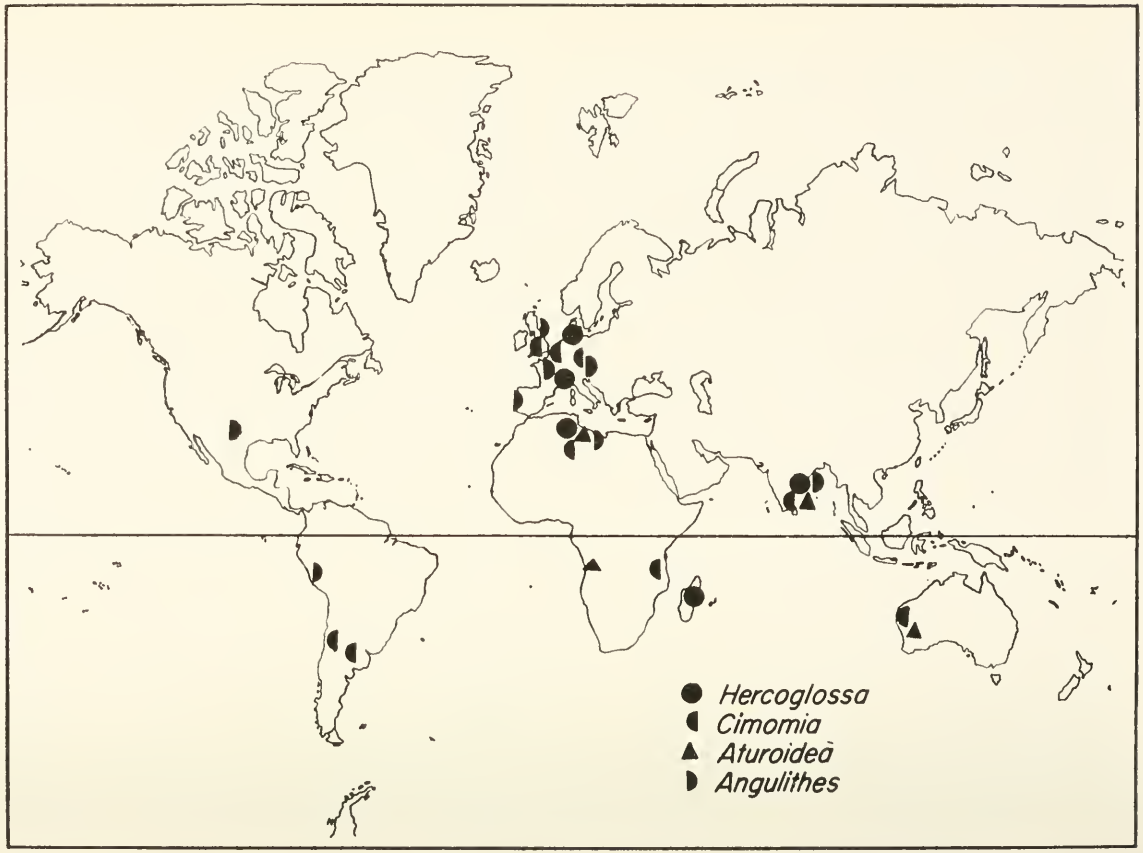

Fig. 29. Geographic distribution of species of the subfamily Hercoglossinae in formations of Cretaceous age.

Fig. 30. Geographic distribution of species of the subfamily Hercoglossinae in formations of Paleocene, Eocene, and Oligocene age.

of increasing sinuosity in the suture ranging from *Cimomia* to *Hercoglossa* to *Aturoidea*. *Angulithes* is probably a special development out of *Cimomia* maintaining an approximate cimomid type of suture but modifying the whorl section to a subtriangular shape rather than rounded. *Cimomia* is readily derived from *Eutrephoceras* with which it is more or less gradational. Since the genera of this subfamily (with the exception of *Angulithes*) are separated on the basis of increasing sinuosity of the suture, it is understandable that there should be gradational forms. These gradational forms are found especially between *Eutrephoceras* and *Cimomia* and between *Cimomia* and *Hercoglossa*. It has been generally assumed that each of these units had a single time of origin and thereafter were distinct genetic stocks (Miller, 1949). An alternative interpretation is, however, possible; that is, that there were several times in the Cretaceous and Tertiary when radiations towards sinuosity of the suture occurred and what is normally included in the genus *Cimomia* is a group of transitional species and not part of a single linear trend. The kind and nature of the data available, however, is not sufficient to test this suggestion. The eutrephoceratid-evolving stock is the parent stock of several radiations (generic groups) of rather diverse morphology. The fact that the genetic potential of the group shows variability in conch shape and suture, is no reason why any number of these variants in suture could not become in themselves genetically distinct, to become part of the species complex included in *Cimomia*.

All four of these genera occur in the Cretaceous and range into the Eocene or Oligocene. *Cimomia* probably includes some Upper Jurassic species. In numbers of species, *Hercoglossa* has 21, *Cimomia* 44, *Angulithes* 32, and *Aturoidea* 11. The relatively large number of species is largely due to "monographic" highs, especially in Tertiary faunas.

Geographically, species of this subfamily are very widespread. The distribution of the Cretaceous species of the subfamily is illustrated on Figure 29, those of the Tertiary on Figure 30. The maps show very well the general overlap in range of all of the genera. None of the forms is sufficiently common at any of the localities indicated so that collections could be made for detailed population studies.

Genus CIMOMIA Conrad, 1866

Cimomia Conrad, 1866a, p. 102.
Cymomia Conrad, 1866b, p. 19.
Cymmomea Conrad, 1868, p. 732.
Cymomia Conrad, 1868, p. 732.
Cimomia Spath, 1927b, pp. 424-428.
Nautilus (Javanoceras) Martin, 1932, pp. 1, 2.
Cimomia Miller and Thompson, 1933, pp. 305-313.
Cimomia Stenzel, 1940, pp. 751-753.
Cimomia Miller, 1947, pp. 39-49.
Cimomia Miller, 1951, pp. 38-47.
Cimomia Haas and Miller, 1952, pp. 329-338.
Type species. Nautilus burtini Galeotti, 1837, from Eocene of Belgium, by original designation. Figured here on Plate 24.

Most of the species of this genus are Tertiary in age (Paleocene — Lower Oligocene) and the Tertiary species have in recent years been thoroughly discussed by Miller and Thompson (1933), Stenzel (1940), Miller (1947), Miller (1951), and Haas and Miller (1952). The very able diagnosis of the genus by Miller (1947, pp. 39-40) is quoted here: "Conch subglobular to subdiscoidal in shape and nautiliconic in its mode of growth. Whorls broadly rounded laterally, rounded ventrally, and impressed dorsally. Umbilicus small; umbilical shoulders low and broadly rounded. Surface of conch marked by growth lines but does not bear ribs or nodes. Septa numerous and each suture forms a broad very shallow broadly rounded or slightly retuse ventral saddle, a broad shallow broadly rounded lateral lobe, a narrower higher rounded lateral saddle (located near the umbilical shoulder), a broad rounded lobe on the umbilical wall, and a fairly prominent internal lateral saddle that extends to a broad rounded dorsal lobe. Siphuncle small, circular in cross section, and orthochoanitic in structure; its position varies considerably in different species, but in no case is it marginal."

Cimomia is in a sense a morphological transitional form, especially in its suture, between *Eutrephoceras* and *Hercoglossa*. In *Eutrephoceras* the suture is essentially straight, or only slightly sinuous; in *Hercoglossa* the suture has well defined lobes and saddles. In both of these genera there are transitional forms to *Cimomia*, reflected especially by the suture. That is, in *Cimomia* there is great variation in the intensity of the lateral

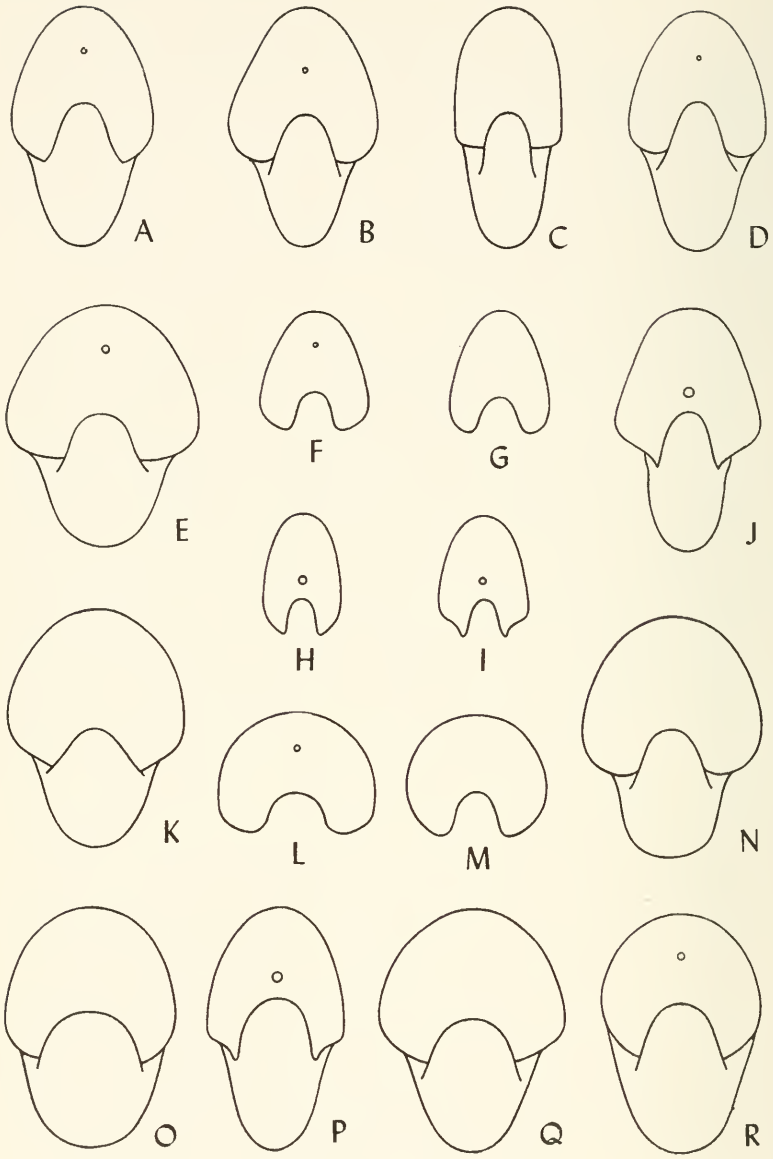

Figure 31

lobe and saddle (Fig. 32). There is likewise much variation in the shape of the conch (Fig. 31). I agree heartily with Miller (1947, p. 41) that *C. kugleri* and *C. vaughani* which have slight lobes in the ventral saddle should be retained in *Cimomia* and not separated from *Hercoglossa*, as *Woodringia* was, solely on this character. In both these species the median lobe is not developed until full maturity .

Most previous authors who have discussed this genus were mainly concerned with the species which occur in Tertiary formations. There are in addition to these, several species of Cretaceous and possibly Upper Jurassic age that should be assigned to this genus. There is first of all *Nautilus romeroi* Ihering (1903, pp. 195-196, fig. 1) of the "Étage Rocanéen" (Upper Cretaceous?) of the territory of Rio Negro in central Argentina, previously mentioned by Miller and Thompson (1935, p. 570) and Miller (1947, p. 41). Recently Miller (1951) has recorded poorly preserved specimens which most surely belong to *Cimomia* from Maestrichtian formation of Senegal. These specimens are too poorly preserved to accurately identify specifically, but there is no doubt as to their generic affinities. From Libya, in

Fig. 31. Cross sections of the conch of *A*, *Hercoglossa harrisi* Miller and Thompson, from Stenzel 1940, fig. 116, diameter 100 mm. ±; *B*, *H. ulrichi* (White) from Stenzel 1940, fig. 116, diameter 170 mm.; *C*, *H? forbesianus* Blanford 1861, pl. 13, fig. 2, diameter 75 mm.; *D*, *H. gardnerae* Stenzel 1940, fig. 116, diameter 145 mm.; *E*, *H. splendens* Stenzel 1940, fig. 120, diameter 73 mm.; *F*, *Hercoglossa orbiculata* (Tuomey) from Miller 1947, fig. 12, height 174 mm.; *G*, *H. meglameryae* Miller and Thompson, from Miller and Collinson 1951, fig. 1B, height 100 mm.; *H*, *Aturoidea vieirai* Miller 1951, fig. 16B, height 130 mm.; *I*, *A. parkinsoni* (Edwards) from Miller 1951, fig. 15A, height 180 mm., the genotype of *Aturoidea*; *J*, *A. paucifex* (Cope), from Miller 1947, fig. 18, diameter 228 mm.; *K*. *Cimomia restali* Miller and Thompson, from Stenzel 1940, fig. 118, diameter 126 mm.; *L*, *C. haltomi* (Aldrich) from Miller 1947, fig. 8, height 104 mm.; *M*, *C. buccinaeformis* Haas and Miller 1952, fig. 2, height 29 mm.; *N*, *C. vaughani* (Gardner) from Stenzel 1940, fig. 118, diameter 59 mm.; *O*, *C. turcicus* (Krumbeck) 1905, pl. 7, fig. 6b, diameter 120 mm.; *P*, *C. haughti* (Olsson) from Miller 1947, fig. 9, diameter 60 mm.; *Q*, *C. subrecta* Miller and Thompson, from Stenzel 1940, fig. 118, diameter 120 mm.; *R*, *C. angustus* (Blanford), from Stoliczka 1866, pl. 93, fig. 42, diameter 40 mm.

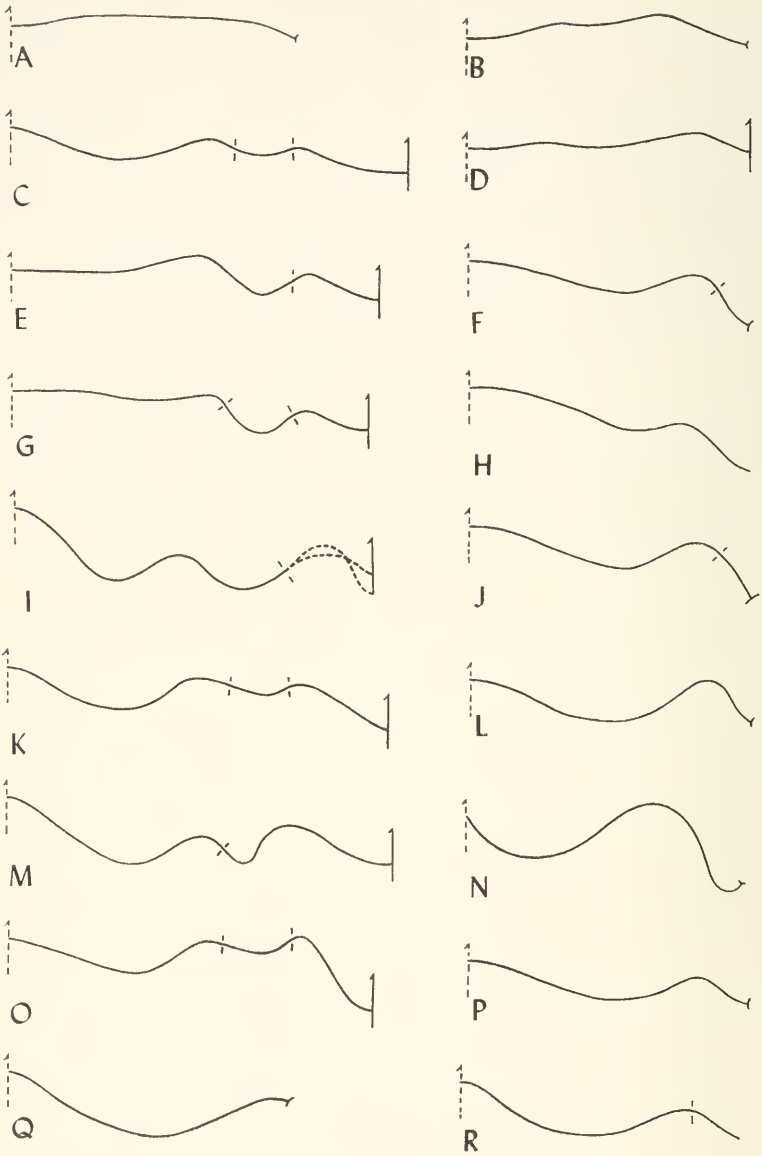

Figure 32

North Africa, Wanner (1902, p. 143) has described *Nautilus jordani,* from formations of Danian age, which is clearly a species of *Cimomia.* Alberici (1940, p. 187) lists the range of this species as Campanian to Danian. The lateral saddle next to the umbilical shoulder in both *C. romeroi* and *C. jordani* is well developed and more distinct than in many lower Tertiary species such as *C. septemcastrensis* Haas and Miller from Lower Eocene of British Somaliland and *C. sahariensis* (Keller) from Eocene? of French Sudan. Another Cretaceous species which should be placed in *Cimomia* is *N. angustus* Blanford (1861, p. 27, pl. 14, figs. 1, 2) from the Ootatoor group (Cenomanian) of south India. Stoliczka (1866, p. 209) records an additional specimen of this species from the Ariyalur group (upper Senonian) of south India. The type specimen of *N. angustus* is a much compressed form with a narrowly rounded venter, and is the most compressed species of *Cimomia* of which a record is available. Stoliczka's specimen (1866, pl. 93, fig. 4, 4a) is a more inflated form and more typical of most species of *Cimomia.* Spengler (1910, p. 145) expressed doubt as to whether Stoliczka's specimen is conspecific with that illustrated by Blanford. Even if these two specimens are not conspecific, they both belong in *Cimomia.* In both specimens the suture has the characteristic pattern found in *Cimomia.*

Fig. 32. Diagrammatic representation of sutures of *A, Eutrephoceras victorianum* (Teichert) 1947, fig. 7; *B, E. dekayi* (Morton) from Reeside, 1924, fig. 1d.; *C, Cimomia wyllei* (Newton) from Haas and Miller, 1952, fig. 5; *D, Eutrephoceras sloani* Reeside from Miller, 1947, fig. 6; *E, Cimomia landanensis* (Vincent) from Miller, 1947, fig. 7A; *F, Cimomia subrecta* Miller and Thompson, 1933, from Stenzel, 1940, fig. 119 (2); *G, Cimomia haltomi* (Aldrich) from Stenzel, 1940, fig. 119 (1); *H, Cimomia pseudobouchardianum* (Spengler) 1910, from Blanford, 1861, pl. 5, fig. 6; *I, Angulithes sowerbyi* (Wetherell) from Stenzel, 1940, fig. 124 (1); *J, Cimomia vestali* Miller and Thompson, 1933, from Stenzel, 1940, fig. 119 (4); *K, Angulithes molli* (Douvillé), from Miller, 1951, fig. 12A; *L, Cimomia macfadyeni* (Haas and Miller) 1952, fig. 4A; *M, Angulithes elliotti* (Stenzel) 1940, fig. 124 (2); *N, A. bakeri* (Teichert) 1947, fig. 3; *O, A. spathi* (Haas and Miller) 1952, fig. 7; *P, A. biyogorensis* (Haas and Miller) 1952, fig. 6; *Q, A. chudeaui* (Douvillé) from Miller, 1951, fig. 10B; *R, A.* sp. from Haas and Miller, 1952, fig. 8B. All figures greatly reduced.

The oldest species of *Cimomia* is thought to be *Nautilus turcicus* Krumbeck (1905, p. 137, pl. 14, fig. 6 a, b) from Upper Jurassic Glandarienkalkes of Libya. This species has an inflated, subglobular, smooth conch and a suture that is slightly sinuous with a rather weak lateral lobe followed by a broad very shallow saddle. As was pointed out above, graditional forms between *Eutrephoceras* and *Cimomia* are known; *N. turcicus* can surely be considered such a form. The shallow, but very distinct lateral saddle lying above the umbilical shoulder shows a clear pattern like that found in *Cimomia,* even though it is only weakly developed.

The distribution and age of the species of *Cimomia* are given below. In addition to these it should be noted that Teichert and Glenister (1952, p. 737) record the presence of undescribed species of *Cimomia* in beds of Upper Campanian to Lower Maestrichtian age from the northwest basin of Western Australia.

DISTRIBUTION OF SPECIES OF THE GENUS CIMOMIA

Species	Stratigraphic Distribution	Geographic Distribution
C. angustus (Blanford) 1861	Cretaceous (Upper)	south India
C. blakei (Avnimelech) 1947	Oligocene	Palestine
C. buccinaeformis Haas and Miller, 1952	Eocene	British Somaliland
C. burtini (Galeotti) 1837	Eocene	Belgium
C. cantabrigiensis (Foord) 1891	Cretaceous (Cenomanian)	England
C. columbinus (Fritsch and Schlönbach) 1872	Cretaceous (Cenomanian)	Bohemia
C. cossmanni (Vredenburg) 1928	Tertiary (Lower)	Pakistan
C. crassiconcha (Vogl) 1908	Eocene	Hungary
C. d'orbignyanus (Forbes) 1846	Cretaceous	Chile
C. ellipticus (Schafhäutl) 1852	Eocene	Bavaria
C. expletus (Zwierzycki) 1914	Cretaceous (Neocomian)	East Africa
C. forbesi (D'Archiac and Haime) 1854	Eocene	Pakistan
C. haltomi (Aldrich) 1931	Paleocene	Alabama (U.S.A.)

Species	Stratigraphic Distribution	Geographic Distribution
C. heberti (Binckhorst) 1861	Cretaceous (Maestrichtian)	Belgium
C. hesperia Miller and Downes, 1950	Eocene	Washington (U.S.A.)
C. hunti Haas and Miller, 1952	Eocene	British Somaliland
C. intuscatenatus (Martin) 1932	Eocene	Java
C. imperialis (J. Sowerby) 1812	Eocene	England
C. jordani (Wanner) 1902	Cretaceous (Campanian-Danian)	Libya
C. karkarensis Haas and Miller 1952	Eocene	British Somaliland
C. kugleri Miller, 1947	Paleocene	Trinidad
C. landanensis (Vincent) 1913	Paleocene	Cabinda, Africa
C. leonicensis (de Zigno) 1881	Eocene	Italy
C. macfadyeni Haas and Miller 1952	Eocene	British Somaliland
C. macrocephalus (Schafhäutl) 1863	Eocene	Bavaria
C. marylandensis Miller and Thompson, 1933	Eocene	Maryland (U.S.A.)
C. mokattamensis (Foord) 1891	Eocene	Egypt
C. negritensis (Olsson) 1928	Eocene	Peru
C. parallelus (Schafhäutl) 1863	Eocene	Bavaria
C. pernambucensis (Maury) 1930	Paleocene?	Brazil
C. phosphaticus (Bédé) 1933	Eocene	Morocco
C. pseudobouchardianum (Spengler) 1910	Cretaceous (Upper)	India
C. pusilla Haas and Miller, 1952	Eocene	British Somaliland
C. romeroi (Ihering) 1903	Cretaceous (Upper)?	Argentina
C. sahariensis (Keller) 1932	Eocene ?	French Sudan
C. seelandi (Penecke) 1884	Eocene	Austria
C. septemcastrensis Haas and Miller, 1952	Eocene	British Somaliland
C. sindiensis (Vredenburg) 1928	Tertiary (Lower)	Pakistan

Species	Stratigraphic Distribution	Geographic Distribution
C. subrecta Miller and Thompson, 1933	Paleocene	Mississippi (U.S.A.), Trinidad
C. sudanensis Miller, 1951	Paleocene	French Sudan
C. tessieri Miller, 1951	Paleocene	Senegal, Africa
C. turcicus (Krumbeck) 1905	Jurassic (Upper)	Libya
C. vaughani (Gardner) 1923	Paleocene	Texas, Alabama (U.S.A.)
C. vestali Miller and Thompson, 1933	Paleocene	Mississippi (U.S.A.)
C. wyllei (Newton) 1925	Eocene	Somaliland

Genus ANGULITHES Montfort, 1808

Angulithes Montfort, 1808, p. 7.
Angulithes Spath, 1927a, pp. 21, 24.
Deltoidonautilus Spath, 1927a, pp. 22, 26.
Deltoidonautilus Spath, 1927b, pp. 427, 428.
Deltoidonautilus Stenzel 1940, p. 759.
Deltoidonautilus Teichert, 1947b.
Deltoidonautilus, Miller, 1947, pp. 64-67.
Deltoidonautilus Miller, 1951, p. 51
Deltoidonautilus Haas and Miller, 1952, pp. 338-344.
Angulithes Kummel, 1953a, p. 8.
Type species. Nautilus triangularis Montfort, 1802 (by original designation in Montfort, 1808, p. 7).

The generic name *Angulithes* remained unused by paleontologists until Spath (1927a) revived it and placed the genus in the family Nautilidae. Spath (1927a, p. 21) listed as genolectotype *'Nautilites' triangularis*, Montfort, in d'Orbigny, 1840, plate 12. However, Montfort (1808, p. 7) specifically designated as type of his genus *'Nautilite triangulaire* du Havre' (Histoire des Mollusques, Buffon, édition de Sonnini, tom. 4, pag. 292, planche 49, 1802). Montfort's illustration of the type of *Angulithes triangularis* (1802, pl. 49) is reproduced here on Plate 25, figure 2. His 1808 illustration of this species is reproduced on Plate 25, figure 1. Both of these illustrations clearly show the triangular outline of the whorl section, the degree of involution,

and the subcentral position of the siphuncle. The sutures on the type illustration (Pl. 25, fig. 2) are undoubtedly oversimplified and wrong. Many specimens of this species from France have been illustrated and recorded; they all have a sinuous suture with a wide lateral lobe and a small saddle near the umbilicus. D'Orbigny (1840, p. 79) described and illustrated *Nautilus triangularis* Montfort including in the synonymy both of Montfort's 1802 and 1808 citations. He likewise listed numerous localities where *N. triangularis* had been found. It is not known whether or not d'Orbigny had access to Montfort's type.

The name combination of *Angulithes triangularis* Montfort (1808) has been validly introduced. There may be a question as to whether the species could be recognized from Montfort's text and illustrations. Even though the suture line as represented on Montfort's (1802) illustration of *Angulithes triangularis* is undoubtedly oversimplified I believe that the species is recognizable.

At the same time that Spath (1927a) revived the name *Angulithes,* he established a new genus *Deltoidonautilus,* type species, *Nautilus sowerbyi* Wetherell, 1836, in J. de C. Sowerby, 1843, p. 35, pl. 627, figs. 1-3. *Angulithes* was thought to be confined to the Cretaceous and *Deltoidonautilus* to the Cenozoic. While Spath (1927a, p. 26) did not diagnose his new genus, he made the following comment: "*Deltoidonautilus* in whorl shape resembles the Cretaceous *Angulithes,* and d'Archiac, and Foord (1891, p. 327) had compared *Deltoidonautilus deluci* (d'Archaic) with *Angulithes triangularis.* The latter, however, with its less sinuous suture line, is more closely allied, via *Ang. fleuriausianus* (d'Orbigny) with the regular Nautilid stock that produced *Pseudocenoceras* in the Cretaceous, as it had given rise before to the less specialized *Paracenoceras* of the *calloviensis* type." The degree of variability in conch shape and sinuosity of the suture are such that the two groups cannot be distinguished (Figs. 32, 33). There is almost a continuous series of species, through the Cretaceous to the Eocene, of involute nautiloids with narrowly rounded to angular venters. *Deltoidonautilus* is placed as a synonym of *Angulithes* (Kummel, 1953a).

Angulithes can be diagnosed as follows: Conch very involute, generally compressed, whorl sides slightly convex, strongly convergent, venter narrowly rounded to angular. Suture moder-

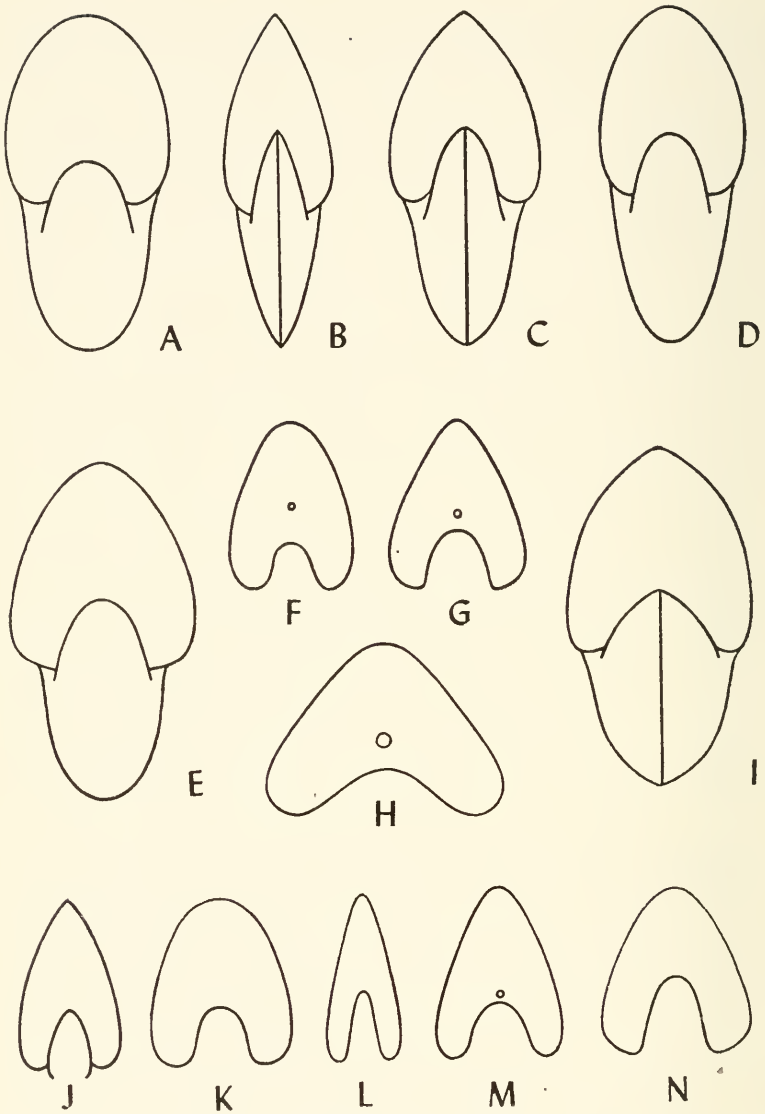

Figure 33

ately sinuous with a narrowly rounded ventral saddle, a broad lateral lobe, a narrow, rounded saddle, and a small lobe on the umbilical shoulder. Siphuncle small and located near the dorsum.

Foord (1891, p. 267) has noted that in the type species—*A. triangularis*—the periphery can be alternately rounded and sharply angular. *Angulithes senegalensis* (Douvillé) has a subangular periphery on the earlier growth stages but at maturity the venter is rounded (Miller, 1951, fig. 14).

Angulithes is in many respects transitional to both *Cimomia* and *Hercoglossa*, differing mainly in its subtriangular whorl section. It is open to question whether this generic group represents a continuous genetic line or trend or whether it may be composed of numerous adaptive trends with this conch shape stemming at several times from either *Cimomia* or *Hercoglossa*. The oldest species of *Angulithes* known to date are *A. arcuatus* (Deshayes) from the Albian of France and England and *A. munieri* (Choffat) from Cenomanian (Cretaceous) of Portugal (Choffat, 1886) and Peru (Schlagintweit, 1912). Kummel (1953a) has recorded an indeterminate species of *Angulithes* from the Pawpaw formation, Tarrant County, Texas. The youngest species is *A. bakeri* (Teichert, 1947, 1952) from Oligocene strata of Australia. There are seven species of *Angulithes* recorded from the Cretaceous (Fig. 29). Most of these are known

Fig. 33. Cross sections of the conch of *A, Angulithes sowerbyanus* (d'Orbigny) 1840, pl. 16, fig. 2, diameter 270 mm.; *B, A. deluci* (d'Archiac) from Miller, 1951, fig. 11A, diameter 128 mm.; *C, A. triangularis* Montfort, from d'Orbigny, 1840, pl. 12, fig. 2, diameter 200 mm., the genotype of *Angulithes; D, A. fleuriausianus* (d'Orbigny) 1840, pl. 15, fig. 2, diameter 192 mm.; *E, A. fleuriausianus* (d'Orbigny) from Stoliczka, 1866, pl. 94, fig. 1a, diameter 100 mm.; *F, A. fleuriausianus* (d'Orbigny) 1840, pl. 15, fig. 3, height 64 mm.; *G, A. sowerbyi* (Wetherell) from Miller 1947, fig. 13A, height 81 mm.; *H, A.* sp. (Haas and Miller) 1952, fig. 8B, height 38 mm.; *I, A. westphalicus* (Schlüter) 1876, pl. 47, fig. 2, diameter 369 mm.; *J, A. tamulicus* (Kossmat) 1897, pl. 6, fig. 6, height 84 mm.; *K, A. elliotti* (Stenzel) from Miller 1947, fig. 13B, height 110 mm.; *L, A. chudeaui* (Douvillé), from Miller 1951, fig. 10A, height 56 mm.; *M, A. rogeri* (Miller) 1951, fig. 13, height 100 mm.; *N, A. molli* (Douvillé), from Miller 1951, fig. 12B, height 72 mm.

from Upper Cretaceous formations of Europe. Species are also known from south India, Peru and Texas (U.S.A.). Tertiary species of *Angulithes* are very widely distributed, being known from North and South America, Europe, Africa, Pakistan, and Australia. Most of the Tertiary species are Eocene in age (Fig. 30).

DISTRIBUTION OF SPECIES OF THE GENUS ANGULITHES

Species	Stratigraphic Distribution	Geographic Distribution
A. aegyptiacus (Foord) 1891	Eocene	Egypt
A. arcuatus (Deshayes) *in* Leymerie, 1842	Albian	France, England
A. bakeri (Teichert) 1947	Oligocene	Australia
A. biyogorensis (Haas and Miller) 1952	Eocene	British Somaliland
A. caheni (Miller) 1951	Eocene	Landana, West Africa
A. calvimontensis (Bédé) 1948	Eocene	France
A. cassinianus (Foord and Crick) 1890	Eocene	England
A. chudeaui (Douvillé) 1920	Eocene	French Sudan
A. deluci (d'Archiac) 1854	Tertiary (Lower)	Pakistan
A. elliotti (Stenzel) 1940	Eocene	Texas (U.S.A.)
A. fleuriausianus (d'Orbigny) 1840	Cretaceous	Europe
A. galea (Fritsch and Schlönbach) 1872	Cretaceous (Upper)	Bohemia
A. haughti (Olsson) 1928	Eocene	Peru
A. hazaraensis (Das-Gupta) 1916	Tertiary (Lower)	Pakistan
A. lamarckii (Deshayes) 1824	Eocene	France
A. lemoinei (Miller) 1951	Eocene	French Sudan
A. molli (Douvillé) 1920	Eocene	French West Africa
A. munieri (Choffat) 1886	Cretaceous (Cenomanian)	Portugal, Peru
A. parabolicus (Schafhäutl) 1863	Eocene	Bavaria

Species	Stratigraphic Distribution	Geographic Distribution
A. rogeri (Miller) 1951	Paleocene	Senegal
A. rollandi (Leymerie) 1846	Eocene	France
A. senegalensis (Douvillé) 1920	Eocene	Senegal
A. singularis (Haas and Miller) 1952	Eocene	British Somaliland
A. somaliensis (Newton) 1925	Eocene	British Somaliland
A. sowerbyanus (d'Orbigny) 1840	Cretaceous (Upper)	France
A. sowerbyi (Wetherell) 1836	Eocene	England
A. spathi (Haas and Miller) 1952	Eocene	British Somaliland
A. subfleuriausianus (d'Archiac) 1850	Tertiary (Lower)	Pakistan
A. tamulicus (Kossmat) 1897	Danian	India
A. togoensis (Miller) 1951	Eocene	Togo
A. triangularis Montfort, 1802	Cretaceous (Upper)	France, England
A. westphalicus (Schlüter) 1872	Cretaceous (Senonian)	Germany

Genus HERCOGLOSSA Conrad, 1866

Hercoglossa Conrad, 1866a, p. 101.
Hercoglossa Hyatt, 1883, pp. 270-271.
Enclimatoceras Hyatt, 1883, p. 270.
Hercoglossa Spath, 1927a, pp. 22, 25, 26.
Hercoglossa Miller and Thompson, 1933, pp. 313-324.
Hercoglossa Stenzel, 1940, p. 743.
Woodringia Stenzel, 1940, pp. 753-759.
Hercoglossa Miller, 1947, pp. 49-64.
Woodringia Miller, 1947, pp. 67-69.
Hercoglossa Miller, 1951, pp. 47-51.

Type species. Nautilus orbiculatus Tuomey, 1854, from Paleocene of Alabama, designated by Hyatt (1883), neotype designated by Miller and Thompson (1933). Neotype refigured here on Plate 27, figs. 1, 2.

The most recent and comprehensive study of this genus is that by Miller and his diagnosis is quoted here (Miller, 1947, p. 50):

"Conch nautiliconic in its mode of growth and subglobular to subdiscoidal in form. Whorls more or less flattened (but typically very broadly rounded) laterally, rather narrowly

rounded ventrally, and deeply impressed dorsally. Umbilicus small; umbilical shoulders rounded. Surface of the test smooth. Septa fairly numerous, and each suture forms a broad very broadly rounded ventral saddle, a deep rounded lateral lobe, a

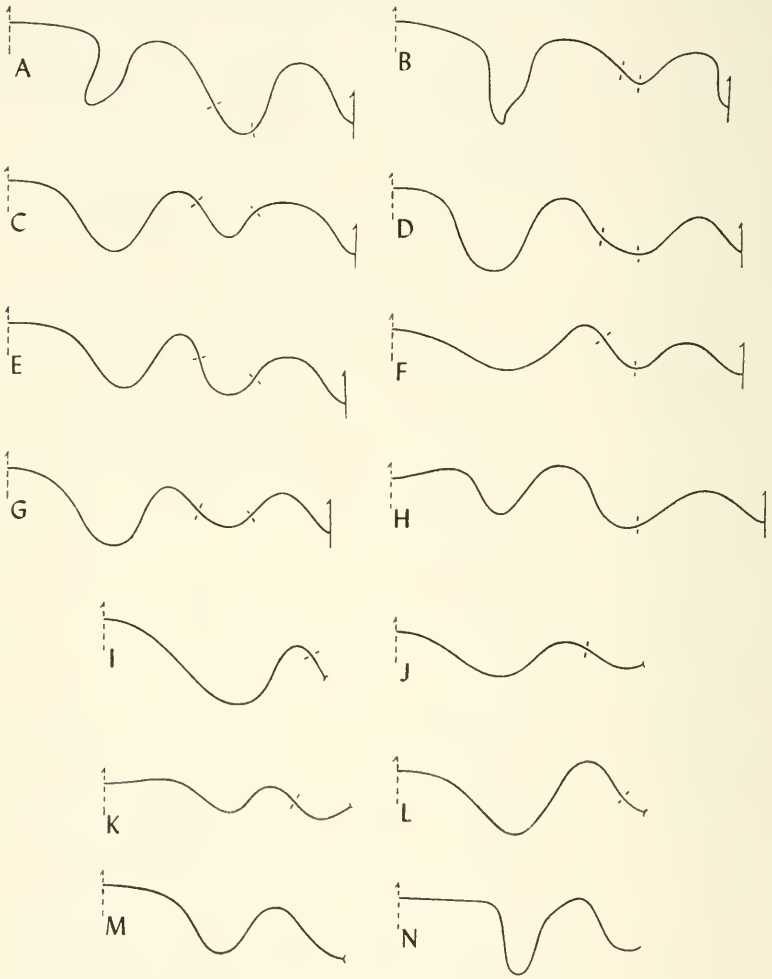

Figure 34

similar lateral saddle, a shallower rather broad rounded lobe on or near the umbilical wall, and a broad rounded internal lateral saddle that extends to a deep rather narrowly rounded dorsal lobe. Siphuncle small and orthochoanitic in structure; its position varies considerably in the different species but in no case is it marginal."

Hercoglossa is closely related to *Cimomia* from which it differs in shape of the suture, to *Angulithes* from which it differs in shape of the whorl section and from *Aturoidea* from which it differs in shape of suture and position of the siphuncle (Figs. 31, 32, 33, 34). *Hercoglossa* is derived from *Cimomia* and incorporates a more advanced or sinuous suture.

The genus *Woodringia* was established by Stenzel for *W. splendens* Stenzel and *W. simiensis* (Vokes) which have a cimomid type of conch in being subglobular, and a hercoglossid type of suture except for a shallow lobe on the venter (Fig. 34). Stenzel differentiates *Woodringia* on the depressed aspect of the whorl section and the presence of a ventral lobe; he considered *Woodringia* to be an independent offshoot from some hercoglossid ancestor. Whereas hercoglossids have in general more compressed conchs than cimomids, there is much variation in the shape of the whorl section (Figure 31). I do not consider the shape of the conch in this particular case to be of any diagnostic value. As to the suture, the presence of the ventral lobe in the ventral saddle is a modification that has occurred in other stocks and has been held to be of not more than specific value. Among species of *Cimomia*, for example, the ventral sad-

Fig. 34. Diagrammatic representation of sutures of *A, Aturoidea pauciflex* (Cope) from Miller and Thompson, 1935, pl. 65, fig. 2; *B, A. vieirai* Miller, 1951, fig. 16-A; *C, Hercoglossa gardnerae* Stenzel, 1940, fig. 117 (1); *D, H. diderrichi* Vincent, from Miller, 1951, fig. 9; *E, H. diderrichi* Vincent, from Stenzel, 1939, fig. 117 (2); *F, H. harrisi* Miller and Thompson, 1937, from Stenzel, 1940, fig. 117 (8); *G, H. orbiculata* (Tuomey) from Stenzel, 1940, fig. 117 (3); *H, H. splendens* (Stenzel) 1940, fig. 121 (1); *I, H. mcglameryae* Miller and Thompson, 1933, fig. 2D; *J, H. maracaibocensis* Miller and Collinson, 1951, fig. 2A; *K, H. simiensis* Vokes, 1937, from Stenzel, 1940, fig. 121 (2); *L, H. popenoei* Miller and Downs, 1950, fig. 1; *M, H. danicus* (Schlotheim) from Blanford, 1861, pl. 13, fig. 4. All figures greatly reduced.

dle is normally well rounded, but in *C. kugleri* Miller and *C. vaughani* (Gardner) a slight median lobe appears at late maturity. Likewise two species of *Aturia* have ventral lobes whereas the "normal" state is a rounded ventral saddle. In *Aturia berryi* Stenzel (1940, p. 764-770, pl. 40, figs. 1-3, text figs. 125 (7) and 126 (2)) the suture is "slightly wavy across the venter so that there is a very shallow ventral lobe in the center flanked on either side by a shallow ventral saddle." However, Miller (1947, p. 88) suggested that the slight ventral lobe may be adventitious in that he could not discern this lobe in any of the other sutures. However, there is another species of *Aturia*, *A. coxi* Miller, 1947 (=*A. narica* Cox 1927, non Vredenburg) from Lower Miocene of Pemba Island in the Zanzibar Protectorate. In this species there is a distinct, rather deep, ventral lobe. I have had the opportunity of examining this specimen in the British Museum and agree with Cox that it belongs in *Aturia*, and I agree with Miller that it is a distinct species. In each of the above cases we are dealing with merely local aberrant species.

Another generic group that displays the same type of variation in the ventral suture is *Pseudaganides*. In this genus the "normal" condition is to have a slight lobe on the venter; however, a few Upper Jurassic species as *P. schlosseri* (Loesch, 1914, pp. 114-118, fig. 8) develop a rounded ventral saddle on the last mature sutures where previously a shallow lobe appeared.

Two species of early Cretaceous nautiloids with sinuous "hercoglossid" sutures are very difficult to evaluate. These are *Nautilus ricordeanus* d'Orbigny and *N. forbesianus* Blanford. The former species (*N. ricordeanus* d'Orbigny) was never illustrated by its author and only very briefly diagnosed. Subsequently Kilian (1915, pp. 17, 18) described and illustrated a specimen from Aptian (Lower Cretaceous) formations of southeastern France which he assigned to *N. ricordeanus*. The specimen is small (44 mm. diameter), involute, compressed, with rounded venter, and flattened sides. The suture is broadly arched over the venter and forms a narrowly rounded V-shaped lobe on the lateral sides. The remaining portion of the suture is not visible in Kilian's illustration. *Nautilus forbesianus* is from Albian strata of south India (Blanford, 1861) and is likewise

an involute, compressed form with an arched venter and the suture has a broad, nearly straight course across the venter and a V-shaped lateral lobe. The character of the suture of these two species suggests affinity to *Aturoidea* more than to *Hercoglossa*. However, the position of the siphuncle is nearer the venter rather than nearer the dorsum as in *Aturoidea*. Cretaceous species of *Hercoglossa* and *Aturoidea* are indeed very rare and any interpretation of these two species can only be tentative pending discovery of new material. It seems that in spite of the apparent specialization of the lateral lobe it would be best to ally these two species, with question, in *Hercoglossa*. The derivation of *Aturoides* from *Hercoglossa* has been a long-accepted, and to me, a correct interpretation. The oldest species of *Aturoidea* is *A. serpentinus* (Blanford) from Senonian strata of south India. *Nautilus ricordeanus* and *N. forbesianus* are thus here considered as part of the earliest radiation from *Cimomia* but perhaps are not part of the main evolutionary line but still congeneric with the principal group.

The species assigned to *Hercoglossa* with their time and geographic range are listed below. The geographic distribution is noted on the maps of Figures 29, 30. Teichert and Glenister (1952, p. 737) record the presence of an undescribed new carinate species of *Hercoglossa* from Eocene strata from the northwest basin of Western Australia.

DISTRIBUTION OF SPECIES OF THE GENUS HERCOGLOSSA

Species	Stratigraphic Distribution	Geographic Distribution
H. danicus (Schlotheim) 1820	Danian	Europe, Asia, Africa
H. diderrichi Vincent, 1913	Paleocene	Senegal
H.? forbesianus (Blanford) 1861	Cretaceous (Albian)	South India
H. gardnerae Stenzel, 1940	Paleocene	Texas (U.S.A.)
H. harrisi Miller and Thompson, 1937	Paleocene	Trinidad
H. immominanda Fleming, 1945	Eocene	New Zealand
H. lamegoi Oliveira, 1953	Paleocene	Brazil
H. madagascariensis Collignon, 1951	Cretaceous (Uper)	Madagascar

Species	Stratigraphic Distribution	Geographic Distribution
H. meglameryae Miller and Thompson, 1933	Paleocene	Alabama (U.S.A.)
H. merriami Dickerson, 1914	Paleocene	California (U.S.A.)
H. orbiculata (Tuomey) 1854	Paleocene	Alabama (U.S.A.)
H. pavlowi (Arkhanguelsky) 1904	Paleocene	Russia
H. peruviana Berry, 1923	Eocene	Peru
H. popenoei Miller and Downs, 1950	Paleocene	Baja, California (U.S.A.)
H.? ricordeanus (d'Orbigny) 1847	Cretaceous (Aptian)	France
H. simiensis Vokes, 1937	Paleocene	California (U.S.A.)
H. splendens (Stenzel) 1940	Paleocene	Texas (U.S.A.)
H. tuomeyi Clark and Martin, 1901	Eocene	Maryland, Virginia (U.S.A.)
H. ulrichi (White) 1882	Paleocene	Ark., Tenn., Ala., Miss., Texas (U.S.A.)
H. walteri Miller, 1947	Paleocene	Alabama (U.S.A.)
H. waringi Miller, 1947	Eocene	Trinidad

Genus ATUROIDEA Vredenburg, 1925

Aturoidea Vredenburg, 1925, p. 9.
Paraturia Spath, 1927a, pp. 22, 26.
Paraturia Spath, 1927b, p. 428.
Aturoidea Vredenburg and Cotter, 1928, p. 18.
Aturoidea Schenck, 1931, p. 450.
Aturoidea Miller and Thompson, 1935, pp. 563-571.
Aturoidea Teichert, 1943, pp. 258-261.
Aturoidea Haas, 1947, pp. 243, 244.
Aturoidea Miller, 1947, pp. 69-77.
Aturoidea Miller, 1951, p. 68.

Type species. *Nautilus parkinsoni* Edwards (subsequent designation by Miller and Thompson 1935, p. 563). Figured here on Plate 28, figures 1, 2.

Miller (1947) has recently thoroughly reviewed the available data on this interesting genus and I find myself in essential agreement with most of his conclusions. His diagnosis of *Aturoidea* is quoted here (Miller 1947, p. 70):

"Conch sublenticular in shape and nautiliconic in its mode of growth; all known forms are large. Whorls compressed, flattened laterally, rounded ventrally, impressed dorsally. Umbilicus closed; umbilical shoulders rounded. Septa asymmetrically sigmoidal; each mature suture forms a very broad high blunt ventral saddle, and on either side of it a deep narrow asymmetrical narrowly rounded lateral lobe, a broad high broadly rounded asymmetrical lateral saddle, a broad rounded lobe with its center near the umbilical seam, and a broad rounded saddle located on the side of the impressed zone and extending to the large rounded V-shaped dorsal lobe. Siphuncle subcentral or subdorsal in position (being nearer the dorsum than the venter, but not in contact with the dorsum), and orthochoanitic in structure — the siphuncular segments are essentially cylindrical in shape and the septal necks are relatively long, being only slightly shorter than the connecting rings."

Only 11 species of *Aturoidea* have been recorded to date and each species is known by one or very few specimens only, a fact unfortunately applicable to most post-Triassic nautiloids. As pointed out by Miller on various occasions *Aturoidea* is very closely related to *Hercoglossa* and *Aturia;* in fact, it is more or less intermediate between them. It differs from *Hercoglossa* in the position of the siphuncle and in the character of the suture. In *Aturia* the dorsal (marginal) position of the siphuncle and the infundibular flexures of the septa are distinctive. The main variations in the suture are in the width and shape of the lateral lobe.

In *A. serpentinus* and *A. schweinfurthi,* both of Upper Cretaceous age, the lobe is well rounded and rather broad. However, in *A. vieirai* from strata of questionable Upper Cretaceous age the ventral flank of the lateral lobe has a distinctive flexure in the lower part making the tip of the lobe narrowly rounded. This same type of modification of the lateral lobe is present in *A. mathewsonii* of Paleocene? age, in *A. paucifex* of Eocene age, in *A. pilsbryi* of Eocene age, and in *A. parkinsoni,* of

Eocene age. The lateral lobe is very narrow and pointed in *A. distans* from the Eocene of Australia.

There are too few specimens or species of *Aturoidea* known to recognize any distinct evolutionary patterns within the group. Species of *Aturoidea* are known from formations of Cretaceous, Paleocene, and Eocene age and have been recorded from England, Austria, India, Africa, Australia, Peru, California, and New Jersey (U.S.A.) (Figs. 29, 30). Teichert and Glenister (1952) report undescribed specimens of *Aturoidea* from Upper Maestrichtian age from western Australia.

DISTRIBUTION OF SPECIES OF THE GENUS ATUROIDEA

Species	Stratigraphic Distribution	Geographic Distribution
A. brunlechneri (Frauscher) 1895	Eocene	Austria
A. distans Teichert, 1943	Eocene	Australia
A. mathewsonii (Gabb) 1864	Paleocene	California (U.S.A.)
A. olssoni Miller, 1947	Eocene	Peru
A. parkinsoni (Edwards) 1849	Eocene	England
A. paucifex (Cope) 1866	Eocene	New Jersey (U.S.A.)
A. pilsbryi Miller and Thompson, 1935	Eocene	New Jersey (U.S.A.)
A. schweinfurthi (Quaas) 1902	Cretaceous (Campanian-Maest.)	Libya
A. serpentinus (Blanford)	Cretaceous (Senonian)	India
A. spathi (Vredenburg) 1928	Eocene	India
A. vieirai Miller, 1951	Cretaceous (Upper?)	Angola

Subfamily ATURINAE Hyatt, 1894

Genus ATURIA Bronn, 1838

Type species. Nautilus aturi Basterot, by subsequent designation, Herrmannsen, 1846, and by virtual tautonymy.

The genus *Aturia*, the sole member of the Aturinae, has received more intensive study than any other group of post-Trias-

Fig. 35. Geographic distribution of species of the genus *Aturia* in formations of Paloecene, Eocene, Oligocene, and Miocene age.

sic nautiloids. The most comprehensive discussion is that of Schenck (1931), and recently Miller (1947) has described the specimens of *Aturia* known from the Americas. Schenck (1931, pp. 448, 449) gives a complete synonymy of the genus and this need not be repeated here. Since Schenck's paper, Stenzel (1935, pp. 553-556) has proposed two new subgenera, *A.* (*Nilaturia*) and *A.* (*Brazaturia*); however, I agree with Miller (1947, p. 81) that these subgeneric categories should not be used. Previously Ihering (1921, p. 76) had proposed the subgenus *Aturia* (*Sphenaturia*) but this name is also suppressed (Schenck, 1931, p. 450; Miller, 1947, p. 81).

This genus is characterized mainly by the infundibular adapical flexure of the septa around the dorsal marginal siphuncle. The conch is usually more compressed and the suture more advaneed than in other Tertiary nautiloids. There is very good ontogenetic evidence of the origin of *Aturia* from *Hercoglossa* through *Aturoidea* (Miller 1947, pp. 78, 79). The genus has been so thoroughly discussed by Schenck (1931) and Miller (1947) that I have nothing of significance to add.

Aturia is truly a cosmopolitan genus, nearly world-wide in distribution and ranges in age from lowest Paleocene (possibly Upper Cretaceous) well into the Miocene (Fig. 35). The named units, "species," of *Aturia* recorded so far are listed below.

DISTRIBUTION OF SPECIES OF THE GENUS ATURIA

Species	Stratigraphic Distribution	Geographic Distribution
A. alabamensis (Morton) 1834	Eocene	Atlantic and Gulf Coastal Plain; Mexico
A. alaskensis Schenck, 1931	Oligocene	Gulf of Alaska
A. angustata (Conrad) 1849	Oligocene-Miocene	Calif.; Wash.; Oregon (U.S.A.)
A. aturi (Basterot) 1825	Miocene	France, Java

Species	Stratigraphic Distribution	Geographic Distribution
A. australis McCoy, 1867	Miocene	Southeast Australia
A. basteroti Benoist, 1888	Oligocene	France
A. berryi Stenzel, 1940	Oligocene	Mississippi (U.S.A.)
A. brazoensis Stenzel, 1935	Eocene	Texas (U.S.A.)
A. brüggeni Ihering, 1921	Eocene ?	Chile (Tierra del Fuego)
A. caroliameghinoi (Ihering) 1902	Eocene ?	Argentina
A. charlesworthi Foord, 1891	Eocene	England
A. clarkei Teichert, 1944	Miocene	Western Australia
A. coxi Miller, 1947	Miocene	Pemba Island, Zanzibar
A. cubaensis (Lea) 1841	Oligocene ?	Cuba
A. curvilineata Miller and Thompson, 1937	Miocene	Florida (U.S.A.), Trinidad, Venezuela, Ecuador
A. dickersoni Schenck, 1931	Paleocene ?	California (U.S.A.)
A. felschi Ihering, 1921	Eocene ?	Chile
A. formae Parona, 1899	Eocene	Italy
A. garretti Stenzel, 1940	Eocene	Louisiana (U.S.A.)
A. grandior Schenck, 1931	Eocene Oligocene	Washington (U.S.A.)
A. grangei Fleming, 1945	Miocene	New Zealand
A. kerniana Anderson and Hanna, 1925	Eocene	California (U.S.A.)
A. koenei Gagel, 1928	Eocene	Germany
A. laticlavia Stenzel, 1935	Eocene	Texas (U.S.A.)
A.? linicentensis Vincent, 1907	Eocene	Belgium
Aturia lotzi Böhm, 1913	Miocene?	S. Africa
A. luculoensis Miller, 1938	Miocene	Angola

Species	Stratigraphic Distribution	Geographic Distribution
A. mackayi Fleming, 1945	Eocene	New Zealand
A. morrissi Michelotti, 1847	Miocene	Italy
A. myrlae Hanna, 1927	Eocene	California (U.S.A.)
A. narica Vredenburg, 1925	Oligocene	Pakistan
A. panamensis Miller, 1947	Eocene	Panama
A. paronai Rovereto, 1900	Oligocene	Italy
A. peruviana Olsson, 1928	Eocene, Oligocene	Peru, Ecuador, Colombia, Venezuela
A. praeziczac Oppenheim, 1903	Paleocene	Egypt
A. preaturi (Cuvillier) 1935	Eocene	Egypt
A. radiata Bellardi, 1872	Miocene	Italy
A. richardsi Miller, 1947	Oligocene	Mississippi (U.S.A.)
A. rovasendiana Parona, 1899	Eocene	Italy, Hungary, Egypt, Palestine
A. somaliensis Haas and Miller, 1952	Eocene	Somaliland
A. tokunagai Shimizu, 1926	Miocene	Japan
A. triangula Stenzel, 1935	Eocene	Texas (U.S.A.)
A. turneri Stenzel, 1940	Eocene	Texas (U.S.A.)
A. vanuxemi (Conrad) 1847	Eocene	New Jersey (U.S.A.)
A. yokoyamai Nagao, 1926	Eocene	Japan
A. ziczac (Sowerby) 1812	Eocene	England

ADDENDUM

The very stimulating monograph by Benavides (1956, Cretaceous System in northern Peru. Am. Mus. Nat. Hist., Bull. 108, pp. 357-493, pls. 31-66) was published when this paper was in page proof. The new genus of nautiloid proposed by Benavides, *Lissoniceras* (type, *Nautilus mermeti* Coquand) is clearly a synonym of *Angulithes* as interpreted in this report.

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PLATES

PLATE 1. CENOCERAS ORBIGNYI

Figures		Page
1, 2	*Cenoceras orbignyi* (Prinz) ..... Two views of type species of the genus *Cenoceras* (=*Nautilus intermedius* d'Orbigny — non Sowerby). From d'Orbigny. X 1.	361

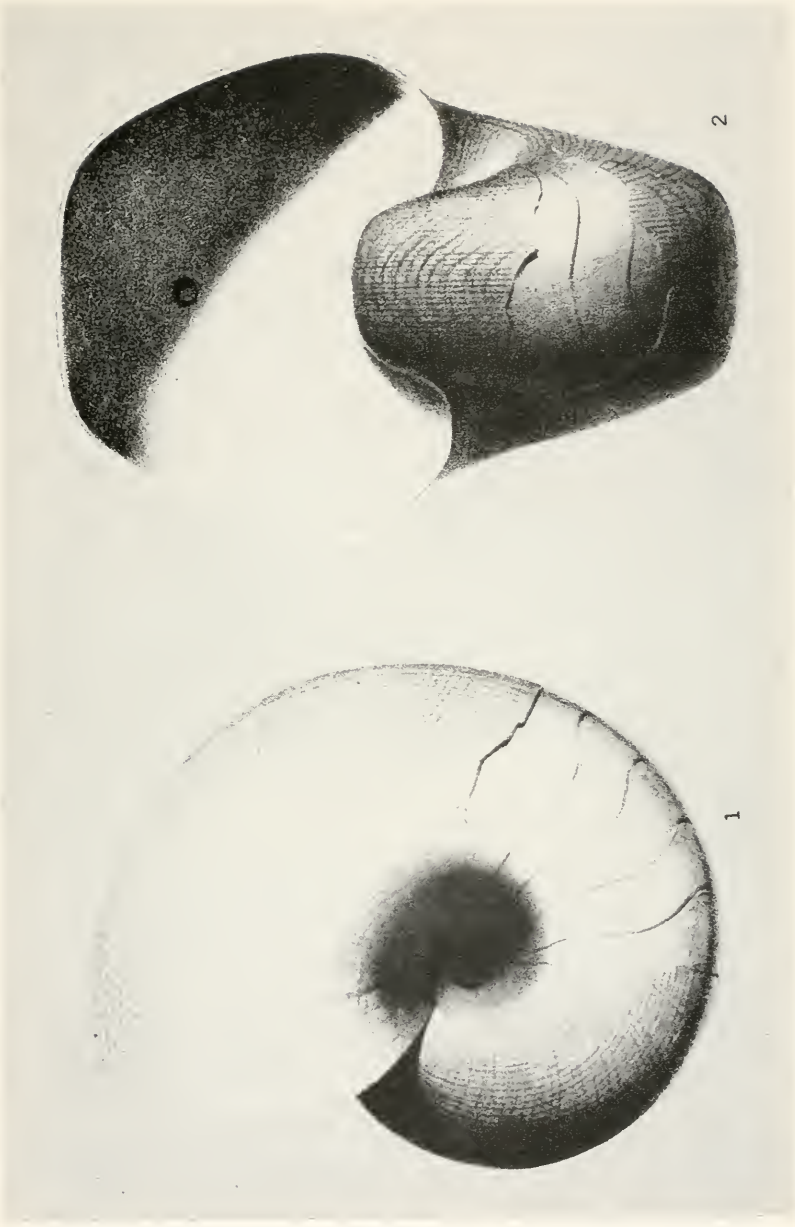


PLATE 1

PLATE 2. CENOCERAS TRECHMANNI

Figures		Page
1-3	*Cenoceras trechmanni* (Kummel) ..... Three views of holotype from Upper Triassic, Carnian, Bed C, Otomita, Hokonin Hills, New Zealand. B.M.N.H. C21947. X 1.	349

PLATE 2

PLATE 3. CENOCERAS STRIATUS

Figures		Page
1, 2	*Cenoceras striatus* (Sowerby) ..... Two views of plesiotype, X 0.60, from Lower Lias, locality unknown. B.M.N.H. 43852 (Sowerby Collection).	362

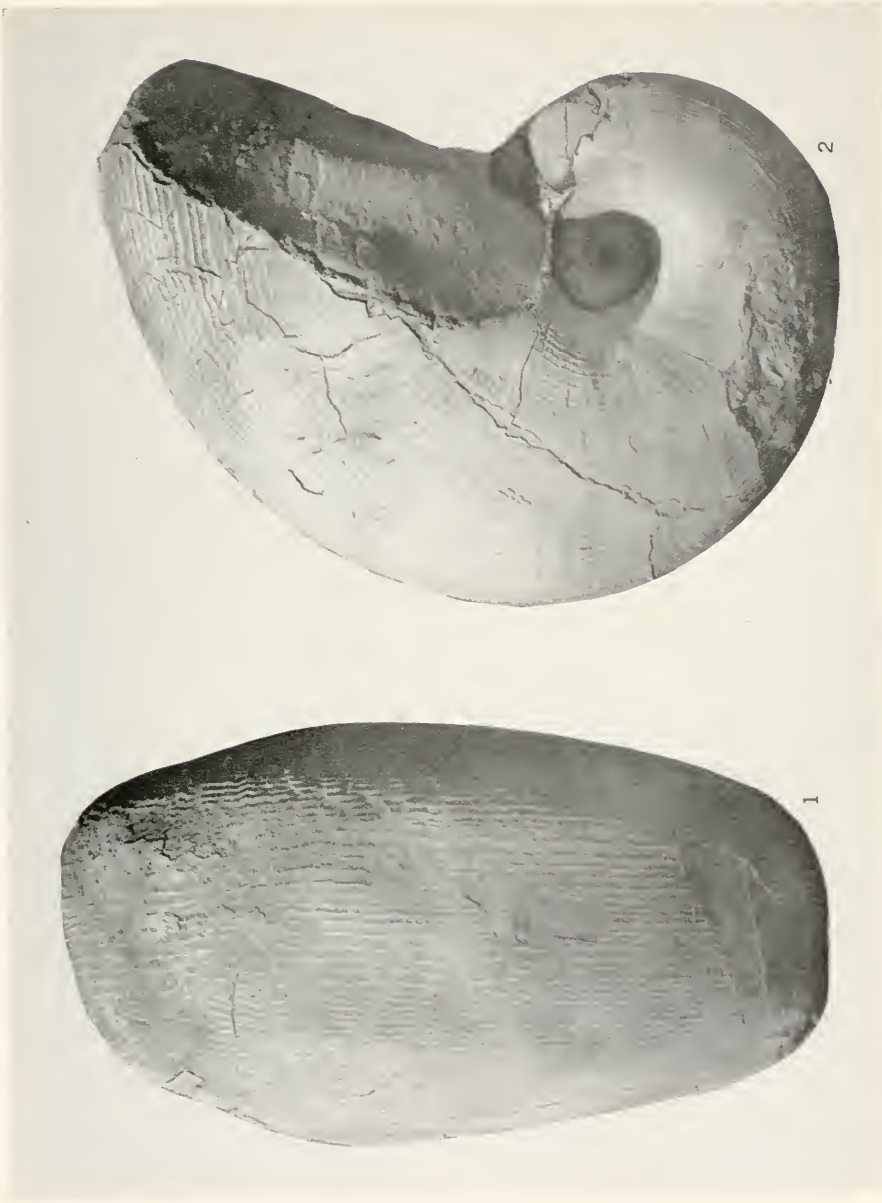


PLATE 3

PLATE 4. CENOCERAS SIMILLIMUS

Figures | | Page

1, 2 *Cenoceras simillimus* (Foord and Crick) 362
Two views of holotype, X 1, from Lias, Charmouth, Dorset, England. B.M.N.H. 39887 (Harrison Collection).

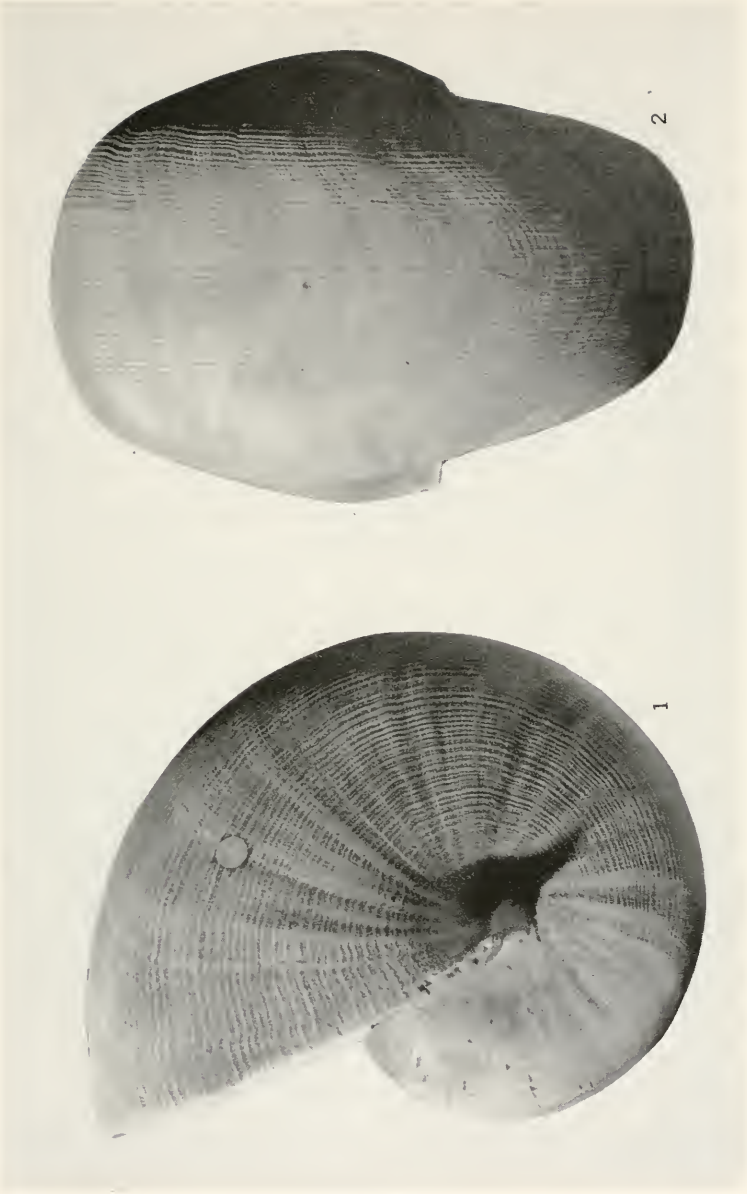


PLATE 4

PLATE 5. CENOCERAS INORNATUS

Figures | Page

1, 2 *Cenoceras inornatus* (d'Orbigny) 362

Two views of plesiotype, X 0.75, from Inferior Oolite, Burton Bradstock, Dorset, England. B.M.N.H. C2843 (Baber Collection).

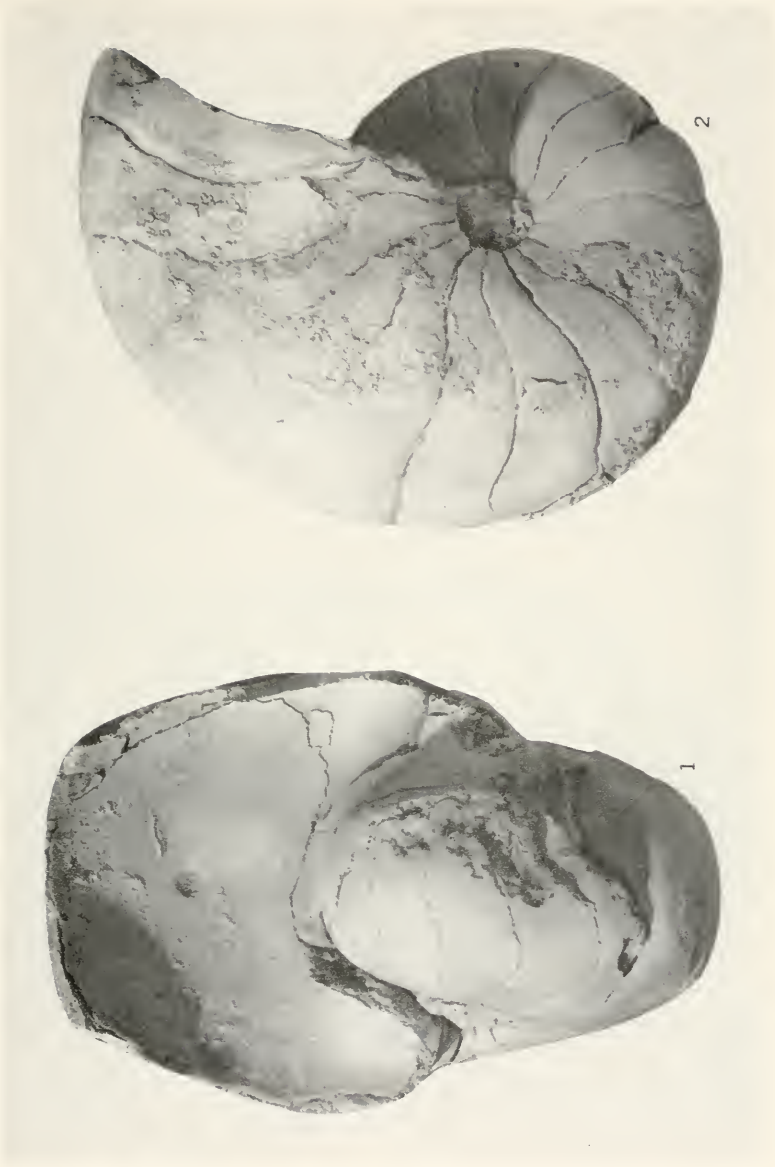


PLATE 5

PLATE 6. CENOCERAS BURTONENSIS

Figures | Page

1, 2 *Cenoceras burtonensis* (Foord and Crick) 371
Two views of holotype, X 0.75, from Inferior Oolite, Burton-Bradstock, Dorset, England. B.M.N.H. 2841 (Baber Collection).

PLATE 6

PLATE 7. CENOCERAS AND SYRIONAUTILUS

Figures		Page
1, 2	*Cenoceras excavatus* (Sowerby) ..... Two views of holotype, X 1, from Inferior Oolite, Dorset. B.M.N.H. 43855 (Sowerby Collection).	369
3	*Syrionautilus libanoticus* (Foord and Crick) ..... Ventral view of syntype, X 1, with mandible on surface, from Upper Cretaceous, Sahil Alma, Lebanon, Syria. B.M.N.H. 83663 (Lewis Collection). Previously figured in Cat. Foss. Ceph., B.M., Pt. 2, p. 371, fig. 82; mandible figured, Ann. Mag. Nat. Hist. [6], vol. 5 (1890), p. 405, fig. 6c; and Cat. Foss. Ceph. B.M., Pt. 2, p. 305, fig. 67c.	433

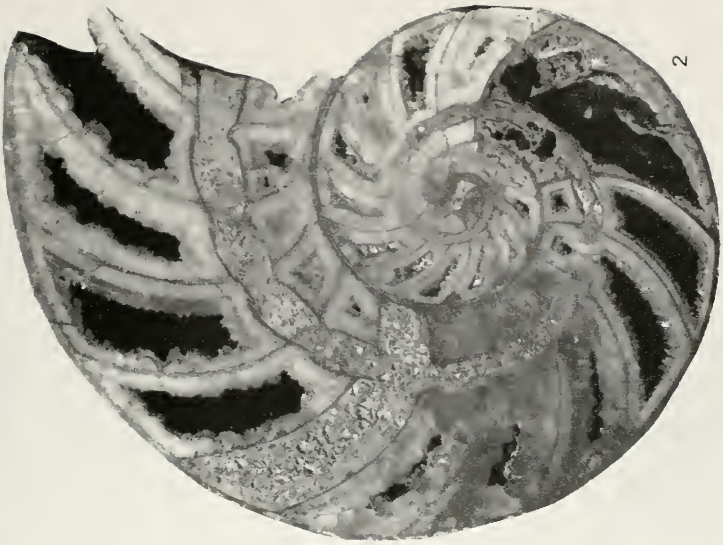
PLATE 7

PLATE 8. PARACENOCERAS AND CENOCERAS

Figures | Page

1 *Paracenoceras hexagonum* (Sowerby) 402
View of polished section of holotype from Corallian Oolite, locality unknown. See Plate 13 for views of external features. B.M.N.H. 43856 (Sowerby Collection MC 529-f2). X 1.

2 *Cenoceras excavatus* (Sowerby) 369
View of polished section of holotype from Inferior Oolite, Dorset. See Plate 7 for views of external features. B.M.N.H. 43855 (Sowerby Collection). X 1.



2

1

PLATE 8

PLATE 9. OBINAUTILUS AND CENOCERAS

Figures | | Page

1, 2 *Obinautilus pulchra* Kobayashi 386
Two views of holotype from Palaeogene Nichinan formation at a cutting between Obi and Aburatsu in Province Hyuga, Japan. X 1. From Kobayashi.

3-6 *Cenoceras rotundum* (Hyatt) 366
Four views of holotype of *Digoniocerас* Hyatt. Locality and horizon unknown; Hyatt labels it "obviously from the Oolite." X 1. M.C.Z. 5217.

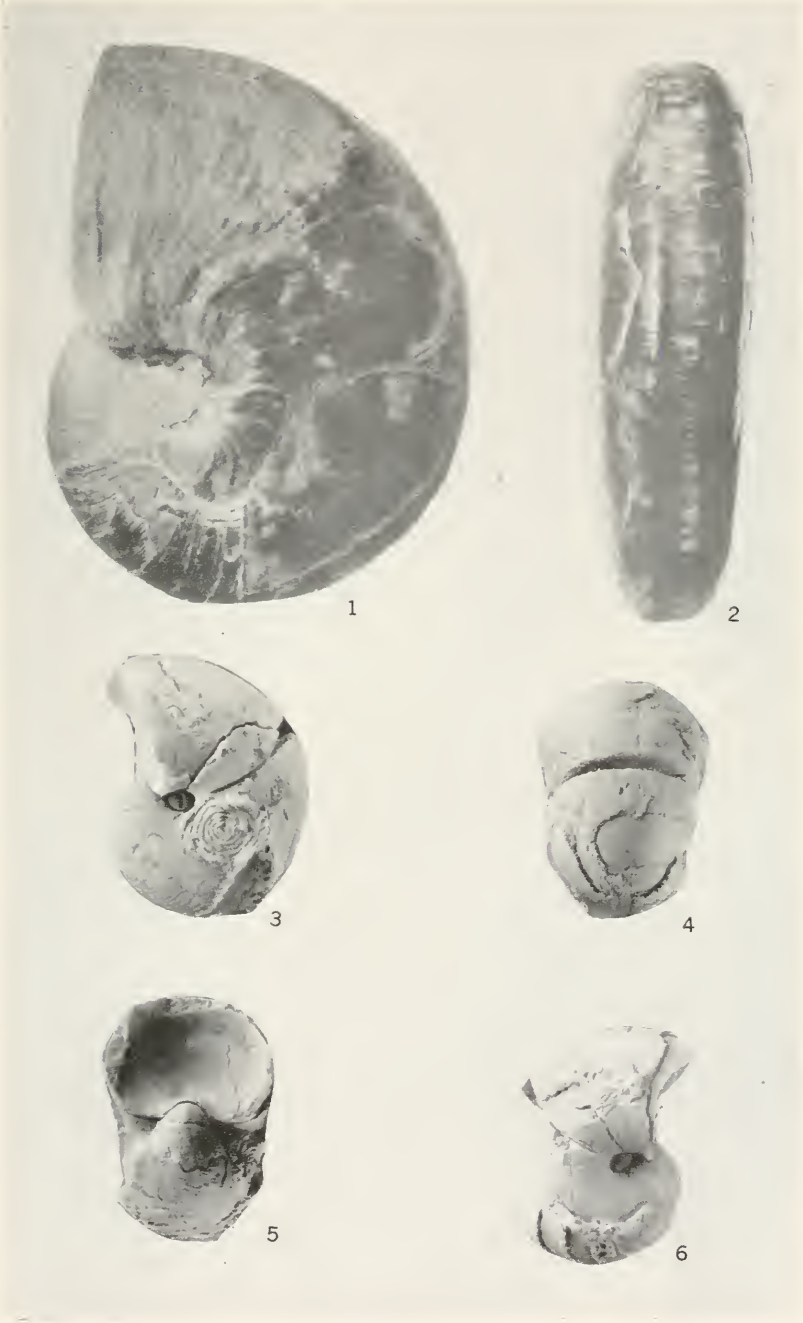


PLATE 9

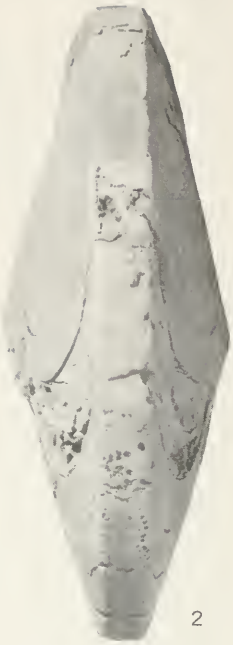
PLATE 10. HEMINAUTILUS AND PSEUDOCENOCERAS

Figures | Page

1, 2 *Heminautilus saxbii* (Morris) 434
Two views of holotype, X 1, from Lower Greensand, Atherfield, Isle of Wight. B.M.N.H. 47019 (Saxby Collection).

3, 4 *Pseudocenoceras largilliertianus* (d'Orbigny) 384
Two views of plesiotype, X 1, from Craie Chloritée, Rouen, France. B.M.N.H. C1016.

1



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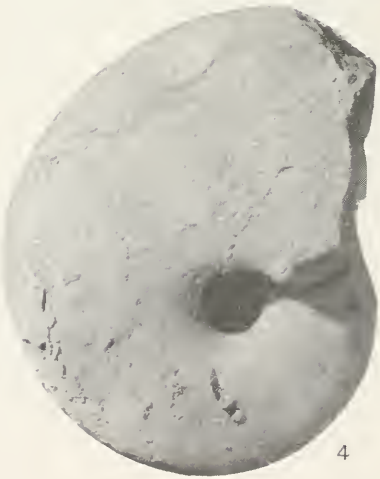


4

PLATE 10

PLATE 11. CARINONAUTILUS ARIYALURENSIS

Figures 1-3 — *Carinonautilus ariyalurensis* Spengler ..... Page 385

Three views of holotype, X 1, from Ariyalur group (Upper Cretaceous), Trichinopoly district, India. From Spengler.

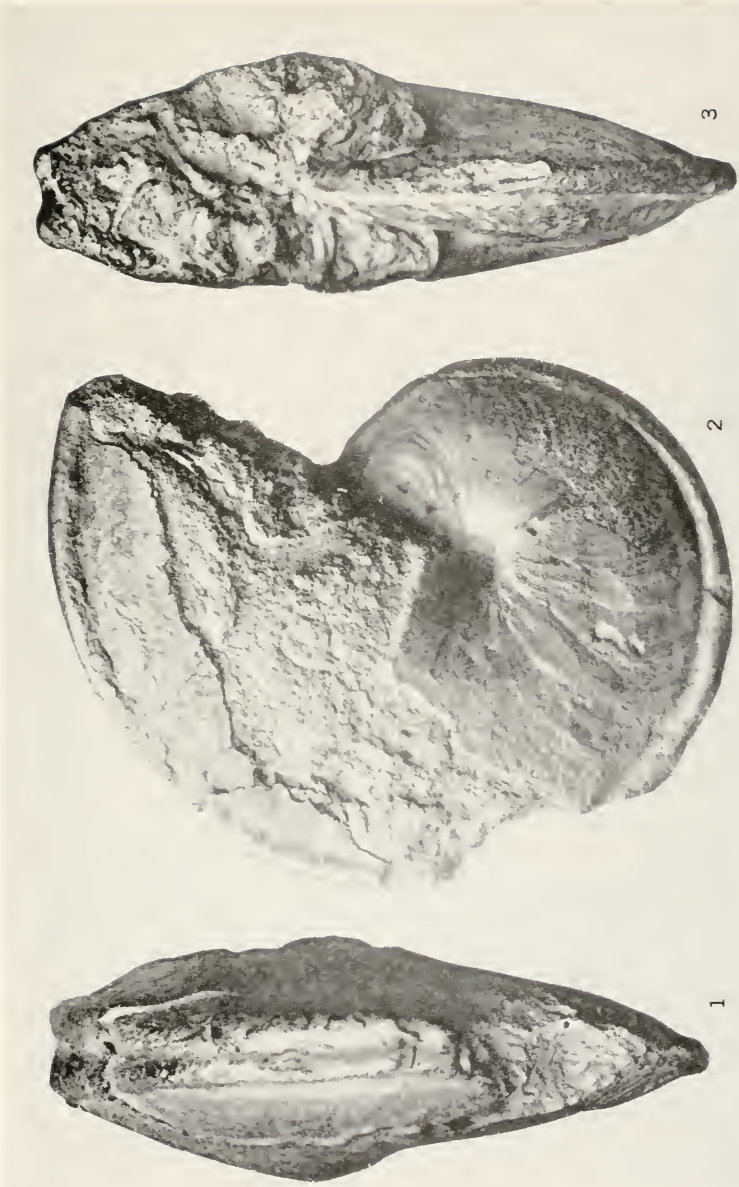


PLATE 11

PLATE 12. PSEUDONAUTILUS GEINITZI

Figures | Page

1, 2 *Pseudonautilus geinitzi* (Oppel) 397
Two views of the holotype, X 1, from Stramberger beds (Upper Jurassic) of Stramberg, Moravia. From Zittel.

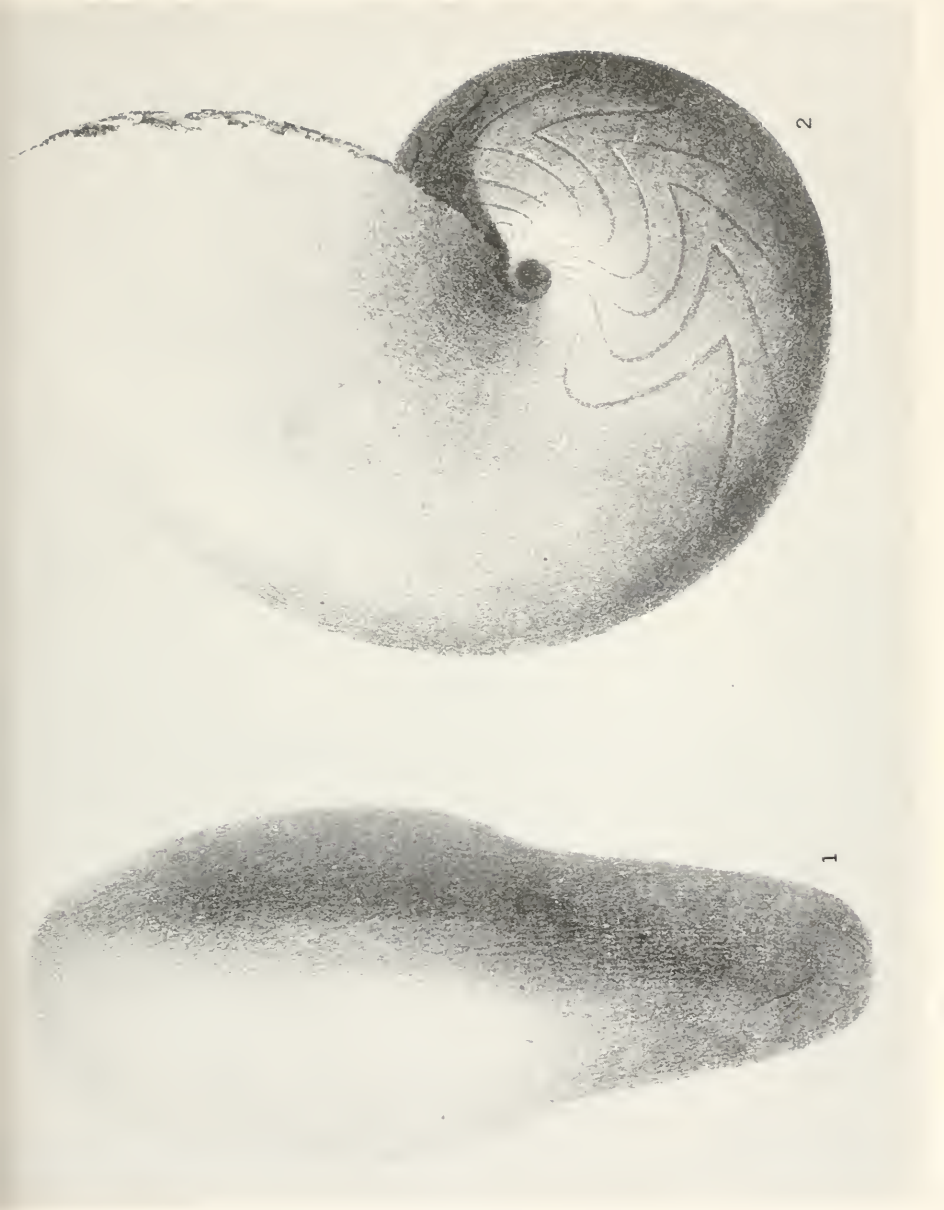


PLATE 12

PLATE 13. PARACENOCERAS HEXAGONUM

Figures | Page

1, 2 *Paracenoceras hexagonum* (Sowerby) 402

Two views of holotype, X 1, from Corallian Oolite, locality unknown. B.M.N.H. 43856 (Sowerby Collection, MC 529-f2).

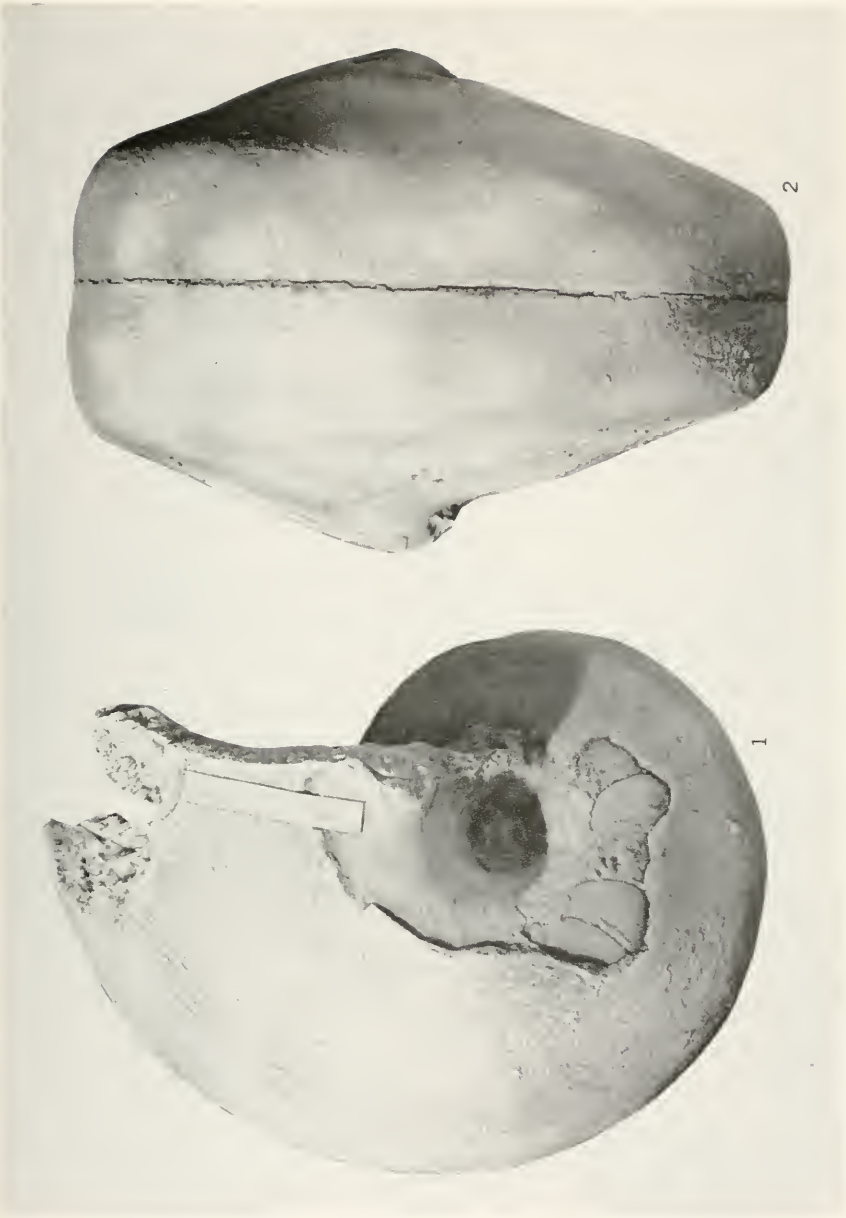
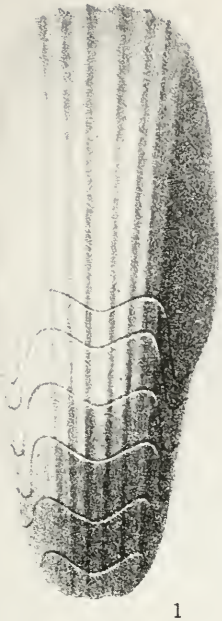


PLATE 13

PLATE 14. AULACONAUTILUS AND SOMALINAUTILUS

Figures		Page
1, 2	*Aulaconautilus sexcarinatus* (Pictet) ..... Two views of holotype, X 0.75, from beds with *Terebratula diphyoides* of Berrias (Ardeche), France. From Pictet.	409
3, 4	*Somalinautilus antiquus* (Dacqué) ..... Two views of holotype, X 1, from Upper Jurassic strata of Somaliland. From Dacqué.	411



1

2

3

4

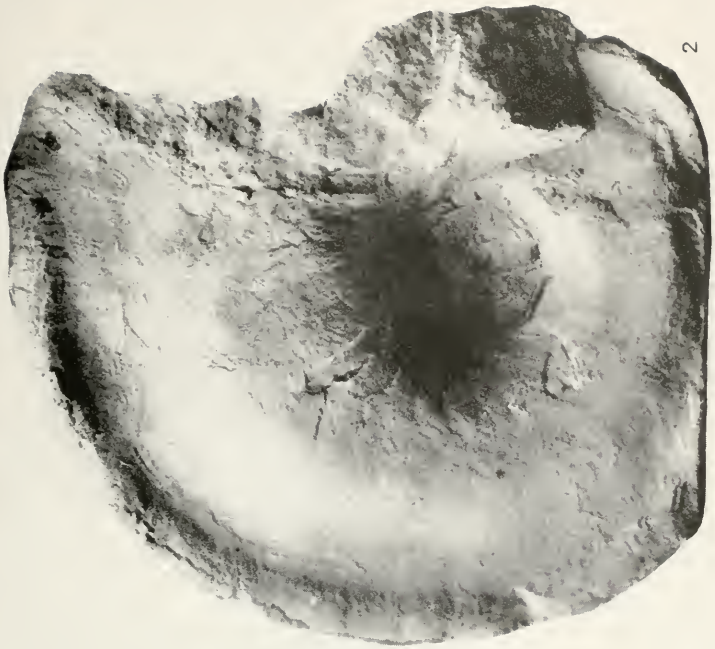
PLATE 14

PLATE 15. TITHONOCERAS ZITTELI

Figures | Page

1, 2 *Tithonoceras zitteli* Retowski 410

Two views of holotype, X 1, from Upper Jurassic strata of Crimea. From Retowski.



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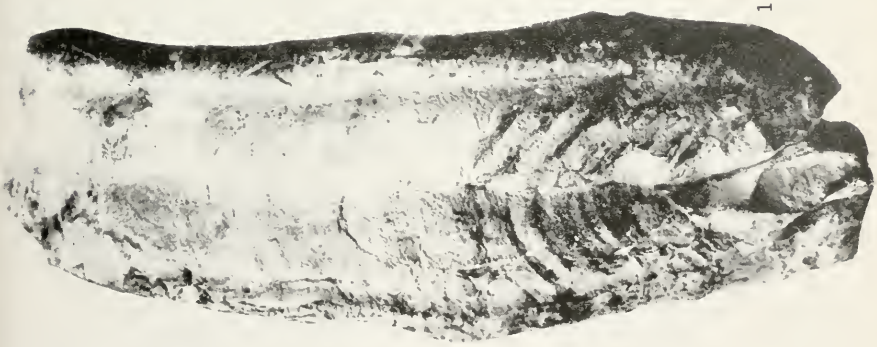


1

PLATE 15

PLATE 16. CYMATOCERAS PSEUDOELEGANS

Figures | Page

1, 2 *Cymatoceras pseudoelegans* (d'Orbigny) 418

Two views of cast of holotype ? (see text page 418) in Museum of Natural History, Paris. X 0.5. B.M.N.H. C5266.

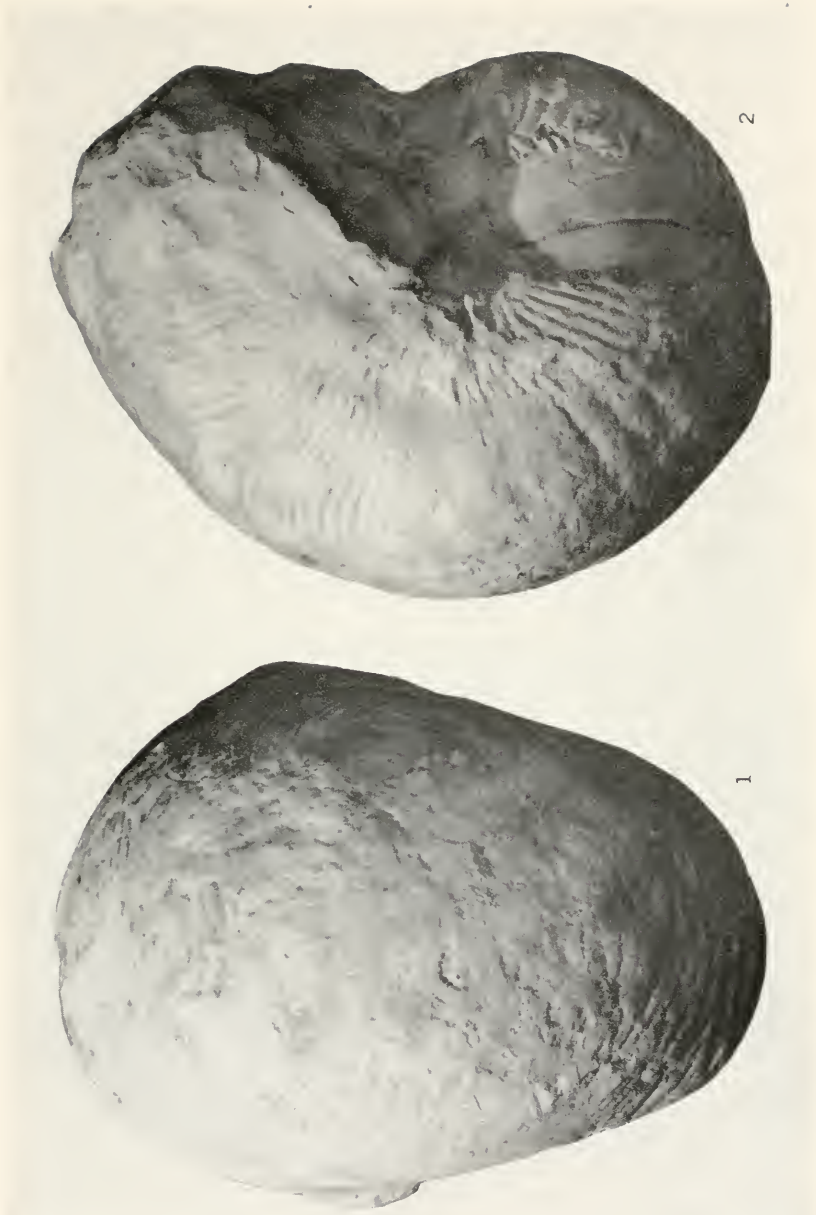


PLATE 16

PLATE 17. PROCYMATOCERAS SUBTRUNCATUS

Figures | | Page

1, 2 *Procymatoceras subtruncatus* (Morris and Lycett) 428
Two views of topotype, X 0.5, from Great Oolite, Minchinhampton, Gloucestershire, England. B.M.N.H. 21275.

PLATE 17

PLATE 18. CYMATONAUTILUS JULII

Figures		Page
1-4	*Cymatonautilus julii* (d'Orbigny) ..... Four views of type species from strata of Callovian age near Montreuil-Bellay and Chauffour, France. From Guéranger.	430

1

2

3

4

PLATE 18

PLATE 19. PARACYMATOCERAS ASPER

Figures | | Page

1, 2 *Paracymatoceras asper* (Oppel) 427
Two views of holotype, X 1, from the Stramberger beds (Upper Jurassic) of Stramberg, Moravia. From Zittel.

PLATE 19

PLATE 20. ANGLONAUTILUS UNDULATUS

Figures | Page

1, 2 *Anglonautilus undulatus* (Sowerby) 430
Two views of topotype, X 1, from Lower Greensand, Nutfield, Surrey (fide L. F. Spath, personal communication). B.M.N.H. 66336. (Sowerby Collection MC 182).

PLATE 20

PLATE 21. EUCYMATOCERAS PLICATUS

Figures | | Page

1, 2 *Eucymatoceras plicatus* (Fitton) 431

Two views of plesiotype, X 0.73, from Lower Greensand, Atherfield, Isle of Wight. B.M.N.H. C335.

PLATE 21

PLATE 22. DELTOCYMATOCERAS LEIOTROPIS

Figures | | Page

1, 2 | *Deltocymatoceras leiotropis* (Schlüter) ..... | 437

Two views of type specimen, X 0.4, from Upper Cretaceous formation of Essen, Germany. From Schlüter, 1876.

PLATE 22

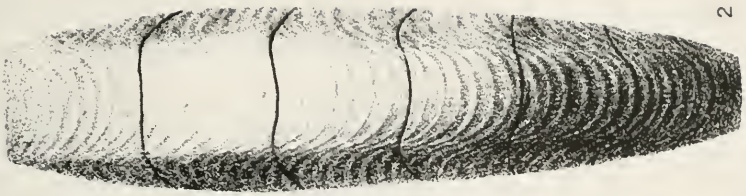
1

2

PLATE 23. EPICYMATOCERAS VAELSENSIS

Figures | Page

1, 2 *Epicymatoceras vaelsensis* (Binckhorst) 438
Two views of type species, X 1, from Upper Cretaceous (Maestrichtian) formation at Limbourg, Belgium. From Schlüter, 1876.



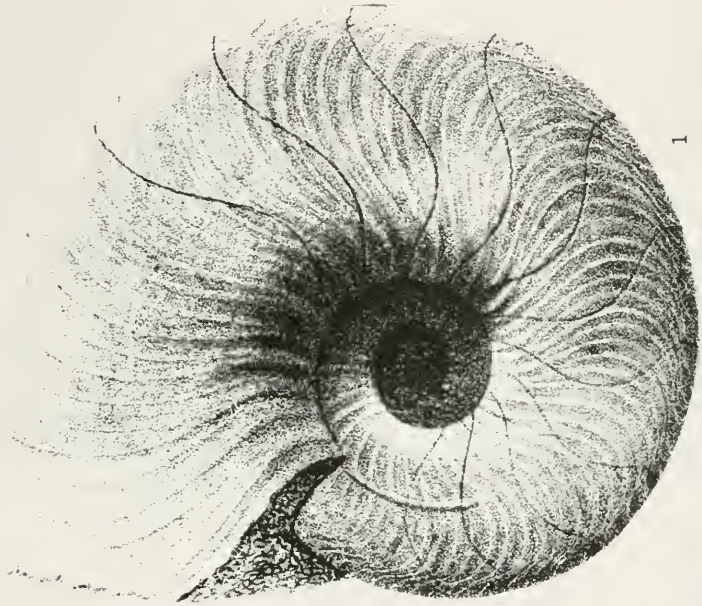


PLATE 23

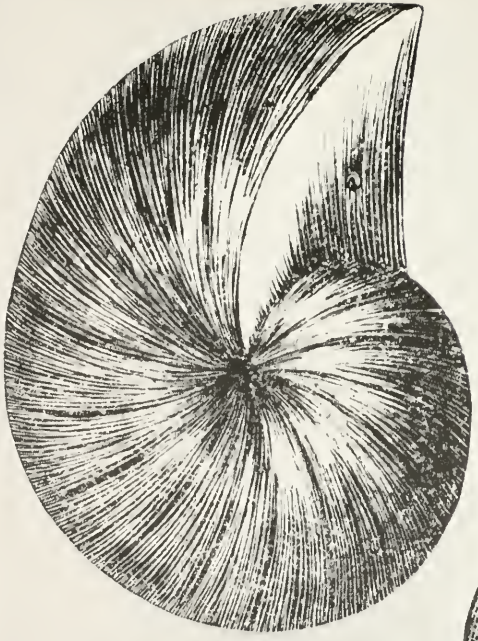
PLATE 24. CIMOMIA BURTINI

Figure | | Page
1 | *Cimomia burtini* (Galeotti) ..... | 445
Reproduction of original illustration of holotype, from the Eocene near Bruxelles, Belgium. X 0.6. From Burtin.

PLATE 24

PLATE 25. ANGULITHES AND "BISIPHYTES"

Figures		Page
1, 2	*Angulithes triangularis* Montfort ..... Figure 1, from Montfort 1808, p. 6; Figure 2, from Montfort, 1802, pl. 49.	452
3	"*Bisiphytes*" *reticulatus* Montfort ..... View of holotype of the genus *Bisiphytes* from beds of uncertain age near Sombernon, France. X 1.	361



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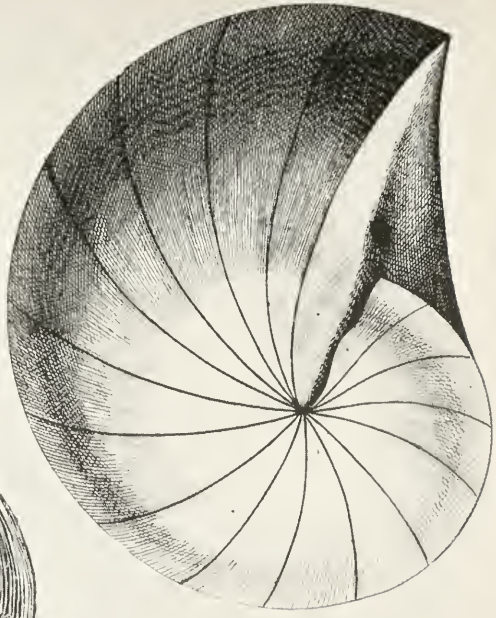

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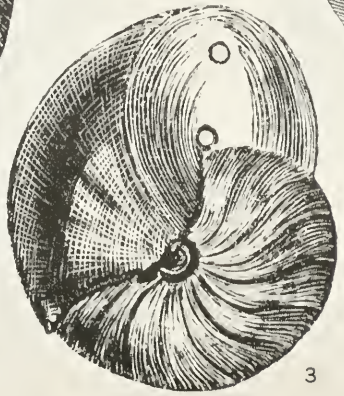


3

PLATE 25

PLATE 26. ANGULITHES TRIANGULARIS

Figures		Page
1, 2	*Angulithes triangularis* (Montfort) ..... Two views of plesiotype, X 0.65, from Craie Chloritée (Cenomanian) Escragnolles, France. B.M.N.H. 37097 (Astier Collection).	452

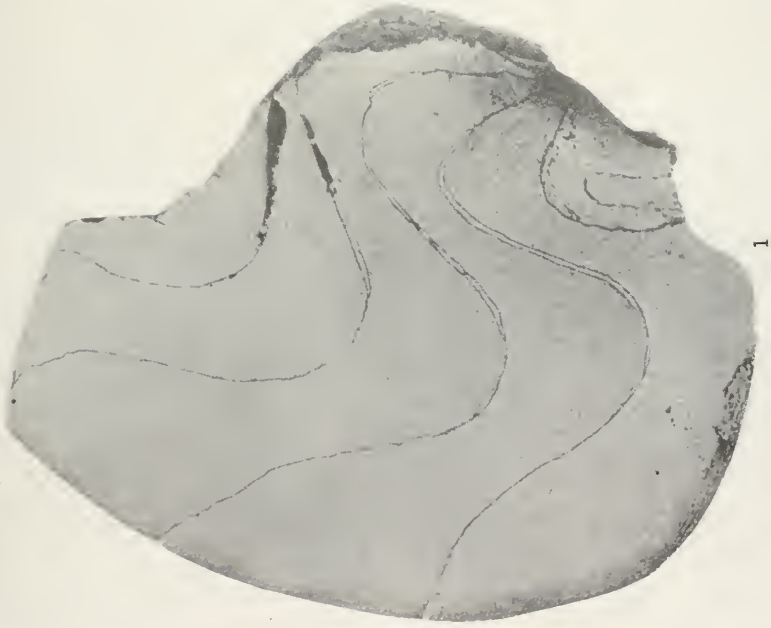
PLATE 26

PLATE 27. HERCOGLOSSA ORBICULATA

Figures | | Page

1, 2 *Hercoglossa orbiculata* (Tuomey) 457
Two views of neoholotype from the Clayton formation on Pine Barren Creek, about 5 miles north of Allenton, Alabama, X 0.5. From Miller.

2



1

PLATE 27

PLATE 28. ATUROIDEA AND PSEUDAGANIDES

Figures | | Page

1, 2 — *Aturoidea parkinsoni* (Edwards) 462
Lateral view (X 0.5) and septal view (reduced) of holotype, from London Clay at Harwich, England. From Edwards.

3, 4 — *Pseudaganides kutchensis* (Waagen) 390
Two views of holotype from beds with *Perisphinctes obtusicosta* of Wanda, Kachh (Cutch) Pakistan. From Waagen.

1

2

3

4

PLATE 28

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